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# SENSORY SPECIALIZATION IN RESPONSE TO ENVIRONMENTAL DEMANDS

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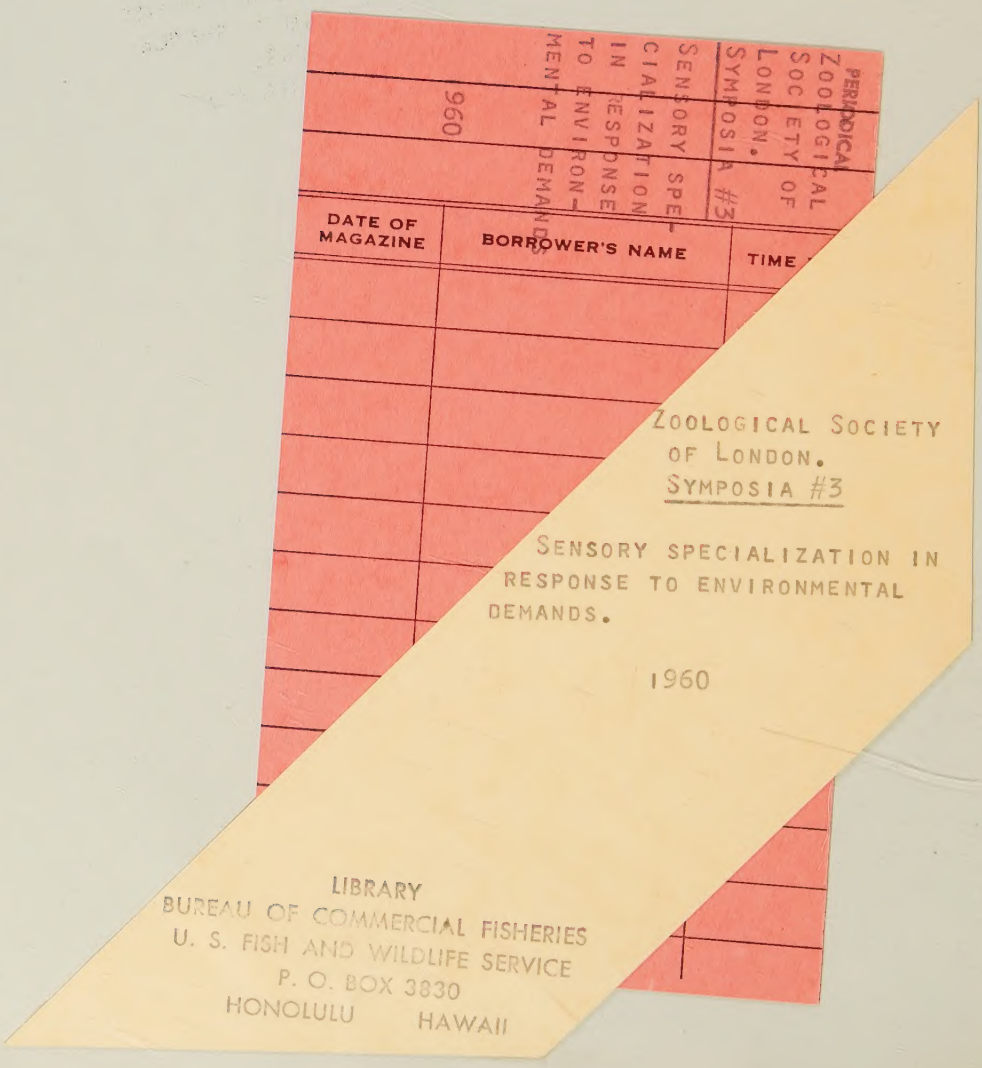
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SYMPOSIA
of
THE ZOOLOGICAL SOCIETY OF LONDON

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# SENSORY SPECIALIZATION IN RESPONSE TO ENVIRONMENTAL DEMANDS

*Proceedings of a Symposium held at*
*The Zoological Society of London*
*Regent's Park, London, N.W.1*
*on 4th March, 1960*

*Edited on behalf of*
*The Zoological Society of London by*
O. E. LOWENSTEIN

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1960

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# INTRODUCTION

BY

O. LOWENSTEIN

*Department of Zoology & Comparative Physiology, Birmingham University*

In introducing this Symposium on Sensory Specialization in Response to Environmental Demands, I should like to point out that the somewhat Lamarckian ring of the title does not mean that the speakers will find it necessary in their description of sensory adaptive mechanisms to infringe Neo-Darwinian orthodoxy.

Adaptive sensory specialization can be of two kinds. It may affect the whole range of sensory modalities in a given animal leading to a successful integration into a highly specialized mode of life. You will find that this is the case in the adaptation of animals to a sub-social or social organization. This is found in locusts and to a more extreme degree in the social Hymenoptera, to be dealt with by Dr Haskell and Dr Kalmus.

The second type of sensory specialization may be confined to one sense organ only, the eye in nocturnal, deep sea or cave animals, or the ear in animals like bats and cetaceans which find their way about by means of sonar. Papers by Dr Denton, Professor Thines and Professor Moehres will deal with this aspect.

Finally, a comparative analysis of sensitivity limits may also reveal instances of adaptation to special environmental circumstances. Dr Marriott will deal with this matter in his paper on the sensitivity limits of photo-receptors.

# THE SENSORY EQUIPMENT OF THE MIGRATORY LOCUST

BY

P. T. HASKELL, B.Sc., Ph.D.

*Anti-Locust Research Centre, London*

The paper reviews the evidence relating to the sensory equipment of the gregarious phase of the desert locust *Schistocerca gregaria* in relation to the demands of flight in swarms. An account is given of the mode of displacement of swarms in relation to the general biology of the locust ; from this it can be concluded that sensory demands relate to the maintenance of steady, stable flight and continued cohesion by locusts in a swarm. The rôle of various sensory systems in the maintenance of flight is discussed together with more detailed evidence of the part played by the compound eyes, receptors on the cervical hair plates and the aerodynamic sense organs in stabilizing flight in various planes of rotation. The structure of swarms and the behaviour of locusts in them is outlined and a hypothesis advanced on the relation of various sensory systems to continued cohesion ; this is thought to be due to a balance between " attractive forces " mediated by visual stimuli and " repellent forces " mediated by acoustic and mechanical stimuli.

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## INTRODUCTION

This symposium is about sensory adaption of animals to their environment. In respect of migratory locusts, intensive and long continued research has demonstrated a wide range of conditions to which these insects are adapted. However, of three major pest locusts, the desert locust, the African migratory locust and the red locust, one of their most important common features is the high level of locomotor drive displayed by gregarious adults, resulting in a large proportion of their life being spent in one environment—the air. Because this leads directly to the most familiar of locust manifestations, the displacement of the populations in the form of swarms, and because it is this manifestation which makes migratory locusts one of the world's major pests, I propose to restrict myself to this aspect of their life history. I shall for the most part consider swarm flight in relation to one species of locust, *Schistocerca gregaria*, the desert locust, although with comparative data where possible on *Locusta migratoria migratorioides*, the African migratory locust, and *Nomadacris septemfasciata*, the red locust.

The environment to which flying swarms are adapted is the air ; during adult life after fledging, the desert locust phase *gregaria* spends a large propor-

tion of its time in flight activity in the swarm. Subjective observations of this activity have contributed much to the theory of directional migration in insects, since an observer's immediate impressions of a flying swarm are almost invariably those of relentless, directed, purposeful flight. Because many such flights end with copulation and oviposition in areas suitable for the development of the eggs and the growth of the emergent hoppers it has often been assumed that the swarm has directed itself by suitable integration of unspecified sensory inputs to the desired environment.

Nothing could be further from the truth ; and because it is germane to later consideration of what end the various sensory inputs to individuals do serve I shall now briefly outline the present hypothesis concerning the movement of swarms in relation to the biology of the locust. This can be most conveniently done by referring to the models erected by Rainey (1959) to illustrate the various possibilities. Figure 1 shows the track of a particular swarm of the desert locust observed for several successive days in East Africa in January, 1954. $P_1$ is the centre of the swarm at 09·15 on 7th January ; pilot balloon observations of wind at Wajir showed that the air in which the swarm was observed could be estimated to have moved to point A by 16·25 hrs the same day, with a speed of 12 Km/hour. If we assume a locust cruising air-speed of 15 Km/hour (a figure consistent with several laboratory and field investigations) and a constant uniform orientation during the period of observation, that is 7 hrs 10 minutes, then at 16·25 hours the swarm would have been situated at some point on the larger circle, whose radius of 107 Km corresponds to the air distance covered in the time and at speeds given above. The actual position on the circle would naturally depend on the orientation selected ; thus constant northerly, easterly and down-wind orientations would have caused the swarm to arrive at points B, C or D respectively.

For the second hypothesis the locusts are considered to be initially concentrated at a point and flying with the same air speed, but independently of one another, on a horizontal plane in a series of successive straight lines with random changes of orientation at exponentially distributed intervals averaging four minutes. On this hypothesis, at 16·25 hrs the swarm would be centred at point A with 95 per cent of the locusts within the smaller circle of diameter 52 Km. The actual observations showed that at 16·25 hrs the swarm was centred at point $P_2$ and its radius was 11–14 Km.

The consideration of this and much other similar evidence leads to the conclusion that while completely random flight orientation in a swarm would give the correct ground-speed and track it would also lead to rapid expansion and dispersal. Mathematical consideration of the dispersion to be expected in a swarm of locusts shows that, with the foregoing assumption of randomly changing independent orientation and known flying speeds, a hypothetical swarm 8 Km in diameter would expand in still air to twice this diameter in 6 hrs, to four times this diameter in 30 hrs and to 6·5 times this diameter in 70 hrs ; observations over this time with an actual swarm of this size showed that after 30 hrs its size was unchanged, while after 70 hrs a doubtful 10 per cent increase was recorded (Rainey, 1958 a). We are thus forced to concede

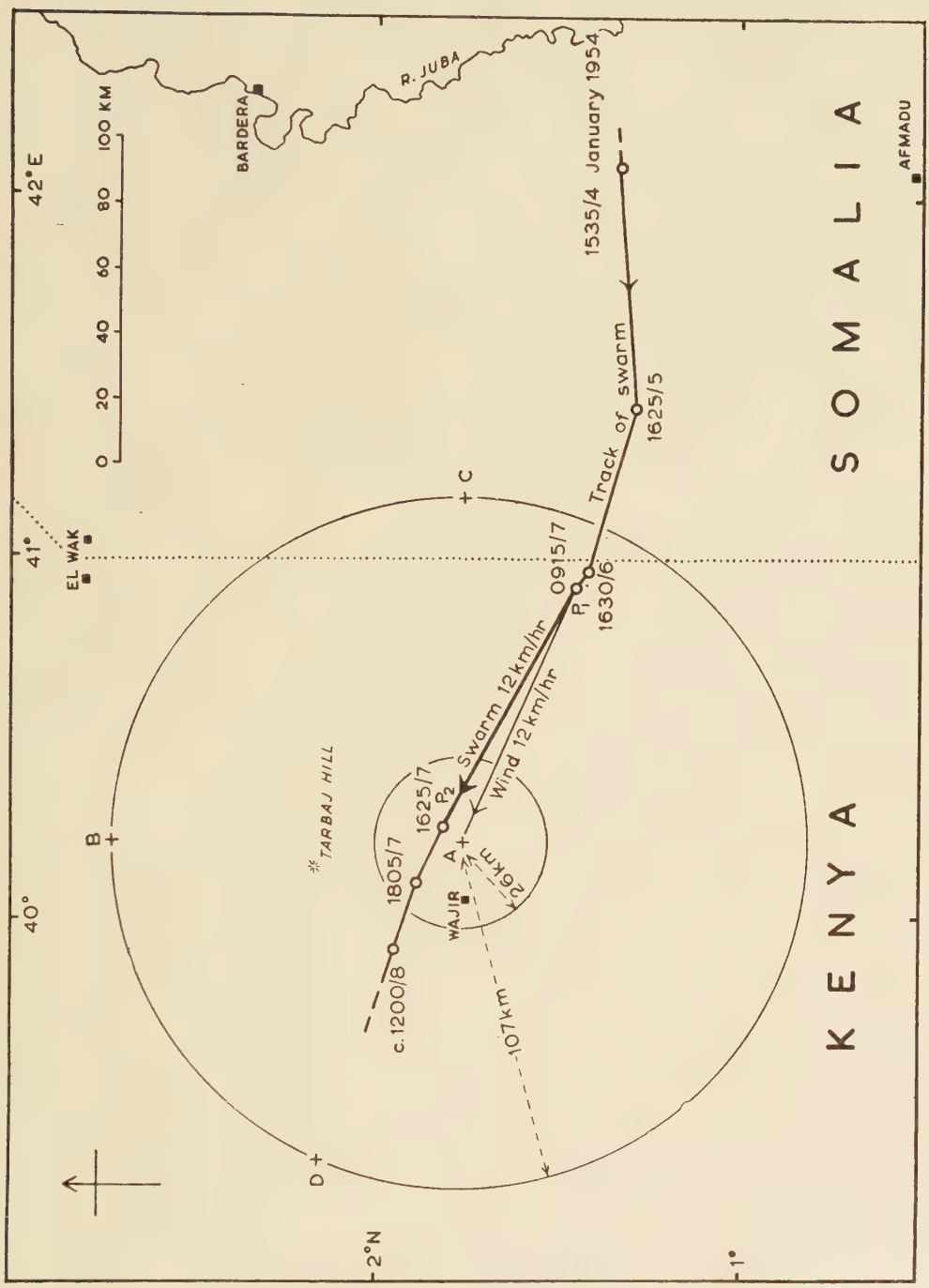


Fig. 1.—Diagram illustrating field data relating to alternative hypotheses of flight orientation in swarms of the desert locust. For explanation see text. (By kind permission of Dr R. C. Rainey.)

to locusts fantastic powers of cohesion, an ability demonstrably dependent on the sensory powers of individual insects.

We must now further consider the implications to the locust of cohesive swarms moving with, and at approximately the speed of, the winds prevailing within 1000 metres of the surface of the ground. Rainey has further developed this side of the story and has summed up his work and those of his collaborators in several important papers (Rainey 1951, 1957, 1958 b). The gist of these, which is our concern here, is as follows : in general and on balance—and the importance of these provisos will presently appear—winds within about 1000 metres of the surface of the ground blow from zones of divergence to zones of convergence and thus locust swarms will tend to collect within such

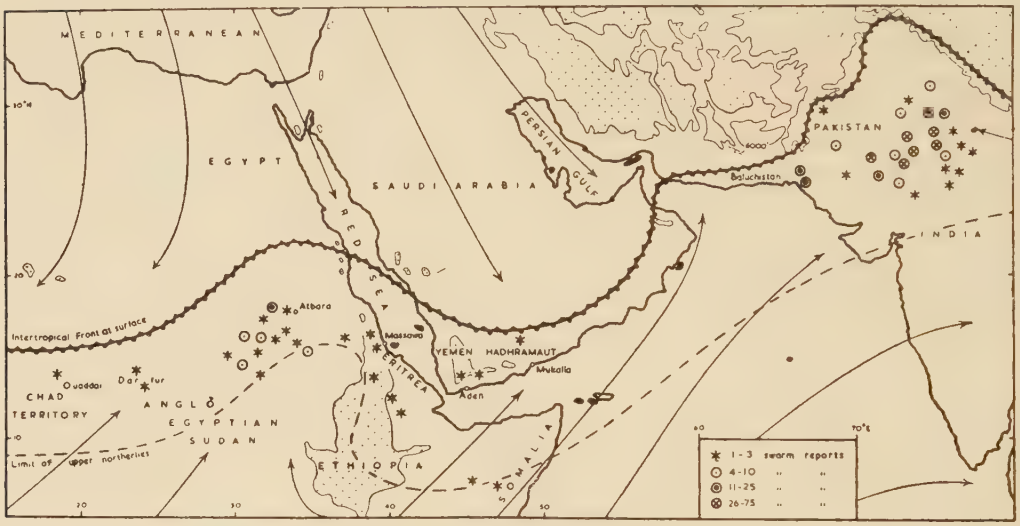


Fig. 2.—Map illustrating the distribution of desert locust swarms in relation to winds and to the semi-permanent Intertropical Convergence Zone, over a period when the latter was effectively stationary. (12–31 July 1950.) (By kind permission of Dr R. C. Rainey and the Editors of " Nature ", London.)

zones (Fig. 2). Zones of convergence are areas across whose boundaries there is an excess of inflowing air ; they are thus areas in which the air rises and in which widespread rain occurs. The apparently purposeful association between swarm movements and rainfall, which is essential for egg and hopper (nymph) development, can thus be seen as an apparent consequence of random flight orientation and down-wind displacement. It will be recalled that a proviso was made in the preceding hypothesis to the effect that wind flow near the ground was in general and on balance into zones of convergence ; not all winds at all times behave in this way. Consequently, if some locust swarms are to stand a reasonable chance of transport to an area of convergence—the copulation and oviposition area—they must all spend as much time as possible in the air. Detailed examination of the flights of many swarms, now being undertaken by Rainey, emphasizes just this point ; the amount of flying done

by the locusts bears no relation to their ultimate net displacement. Indeed, records exist to show that some swarms have been displaced on a closed track so that many days after leaving one place they cross their own path again.

This need to keep as long as possible in the air gives rise to a basic problem of fuel ; it is well known from the work of Krogh & Weis-Fogh (1951) and Weis-Fogh (1952) that locusts use fat as fuel. Carbohydrate is used at the beginning of flight because it can be more quickly mobilised and used, but fat combustion supplies probably 80 per cent of the energy requirements. The need for long continued locomotor activity, for reasons given above, makes economical use of fuel one of the prime necessities of flight behaviour in locusts. Weis-Fogh (1952) showed that in the desert locust metabolic rate increased approximately as the square of the speed and air-speeds of 2·5 metres/second were two or three times less expensive than those of 3·5 m/s. Thus economical flight is slow-and-steady flight—the mechanism must be governed to run at a steady speed. With a steady power output instability in any plane involves loss of height with consequent further expenditure of energy to make this up. Having regard to these facts about locust swarm flight it is clear that the main sensory demands made on a flying locust are related to the maintenance of steady stable flight and to the necessity of coherence with other locusts during flight.

## MAINTENANCE OF FLIGHT

The classical investigations of Weis-Fogh (1956 a, 1956 b) and Weis-Fogh & Jensen (1956) are of course pre-eminent in the field of locust flight and summarize present knowledge. It is therefore only necessary in this section of the paper to draw attention to the broad outlines of the sensory systems involved in locust flight maintenance except where there is something new to add. In normal locusts, flight is initiated by a take-off jump ; this jump, in the great majority of cases, takes place into wind, the orientation for maximum lift. Locusts on the ground can detect wind with a number of sense organs, including the aerodynamic sense hairs on the frons and vertex, first described by Weis-Fogh (1949), the long hair sensillae on the anal cerci (Haskell, unpublished) and various hair sensillae on the thorax and pronotum. Of these receptors the hair sensillae on the anal cerci are the most sensitive, responding to air flows as low as 4 cms per second, but they are non-directional and few in number. The thoracic and abdominal hairs only respond to rather fast wind flow and are non-directional. The aerodynamic sense organs, on the other hand, as recent studies by Haskell (1959 a, 1960) show, respond to wind flows from 1 metre per second upwards ; furthermore, the direction of movement of the hair is important, as shown in Fig. 3. The arrangement of certain hairs is such that wind flow along the line of the longitudinal axis of the insect would stimulate them ; this allows orientation into the wind while the locust is on the ground. If these hairs are covered the power is very largely lost. The take-off jump into the wind leads to loss of tarsal inhibition (Fraenkel, 1932) and wing flapping commences. The aerodynamic sense organs are further stimulated and the antennae and fore-legs take up the flight posture ; with passage of air over the wings the maintenance system

postulated by Weis-Fogh (1956 b) of " wind-over-the-wings " is also activated, leading to assumption of the complete flight posture. The wing cycle is maintained while the aerodynamic sense organs are sufficiently stimulated, as they are if the relative wind exceeds 2 metres per second. This is well above the threshold of certain of the hairs and presumably a number are stimulated at the higher air flow. However, once flight has commenced, these cephalic hairs can be occluded without stopping the wind flapping cycle, which is presumably kept going by the " wind-over-the-wings " receptors, which have not yet been localised.

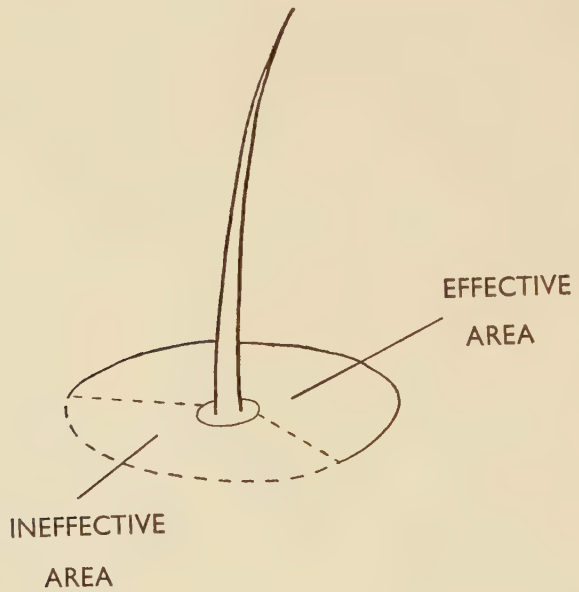


Fig. 3.—Diagram to illustrate the direction of movement of locust cephalic hair necessary to produce sustained impulse discharge in the neurone ; only movement towards the perimeter of the " effective area " causes a discharge.

## CONTROL OF STABILITY

Once in the air, flight must be stabilized against rotations in the rolling, yawing and pitching planes ; in insects, active stabilization movements must be made continuously to counteract instability. The degree of compensation possible in locust flight is illustrated by the fact that in field experiments in Africa it has been shown (Haskell, unpublished data) that *Schistocerca* adults whose abdomens have been removed at about the second segment and whose legs have been cut off are still capable of steady level flight for distances over 100 metres ; these experiments also illustrated that the sense organs necessary for maintenance and stability control must reside only on the head or thorax.

During these field experiments the flight of blinded locusts was studied. Progressive occlusion of both compound eyes led to more and more unstable flight during tests carried out in sunlight with a reasonably steady wind ; the

instability seemed most marked in the rolling plane. Complete blinding did not interfere with the initiation or maintenance of flight and several of these locusts were observed to fly further than 100 metres, gaining height and apparently stable ; but in most cases instability became apparent after several seconds of flying and the locust went into a spin and crashed. These observations, considered together with those of Rainey & Ashall (1953) on a probable

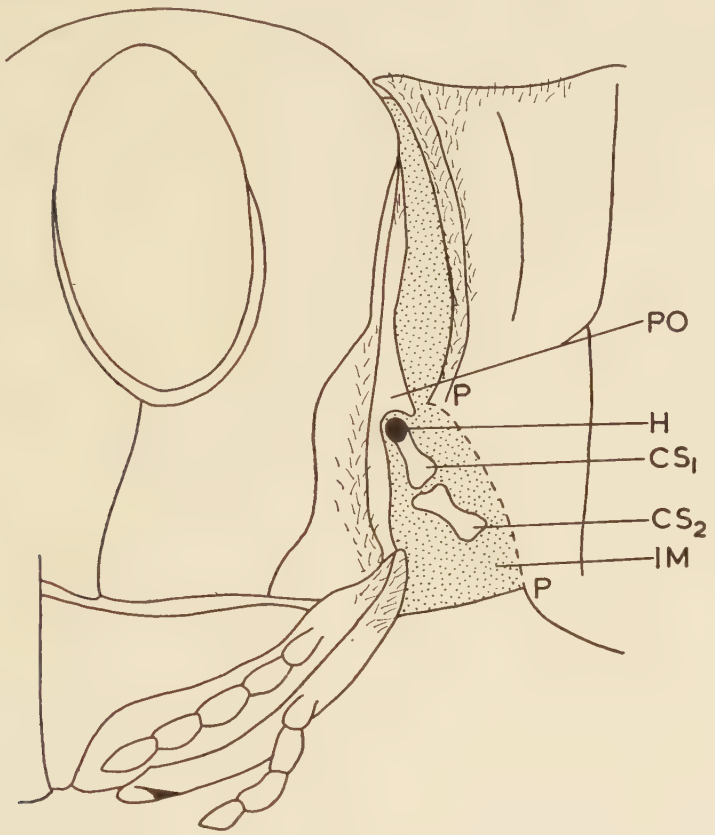


Fig. 4.—Diagram of part of the head and prothorax of *Schistocerca gregaria* with the head pulled slightly to one side to reveal the intersegmental membrane, cervical sclerites and hair plate. Some of the hairs present on the prothorax and head are also shown. P-P, pronotum cut away to reveal the cervical sclerites ; $CS_1$, $CS_2$, first and second cervical sclerites ; the second sclerite articulates with the region of the pronotum that has been removed ; H, hair plate ; PO, post-occipital region of the head ; IM, intersegmental membrane. (By kind permission of Dr L. J. Goodman and the Editors of " Nature ", London.)

dorsal light reaction in locusts, infer that one of the functions of the compound eyes is related to a flight stabilizing system. Recent work by Goodman (1959) has confirmed and amplified this ; she arranged locusts in a frame which enabled them to flap their wings and rotate about their longitudinal axis. Under these conditions normal locusts rotated until the dorsal ommatidia were maximally illuminated, then continued to fly in this position. Alteration

of the light source relative to the ommatidia produced a head rotation which was followed by body movement until both were in alignment. The maintenance of this alignment depends on several sets of proprioceptors, notably the hair plates borne at the tip of the first cervical sclerite and certain hair sensillae on the anterior edge of the prothorax (Fig. 4). Goodman found that the ability of the locust to maintain its orientation to light was reduced if the prothoracic hairs were destroyed and was made almost impossible if the hair plates were destroyed. If both sets of receptors were destroyed, the locust constantly rotated in its frame.

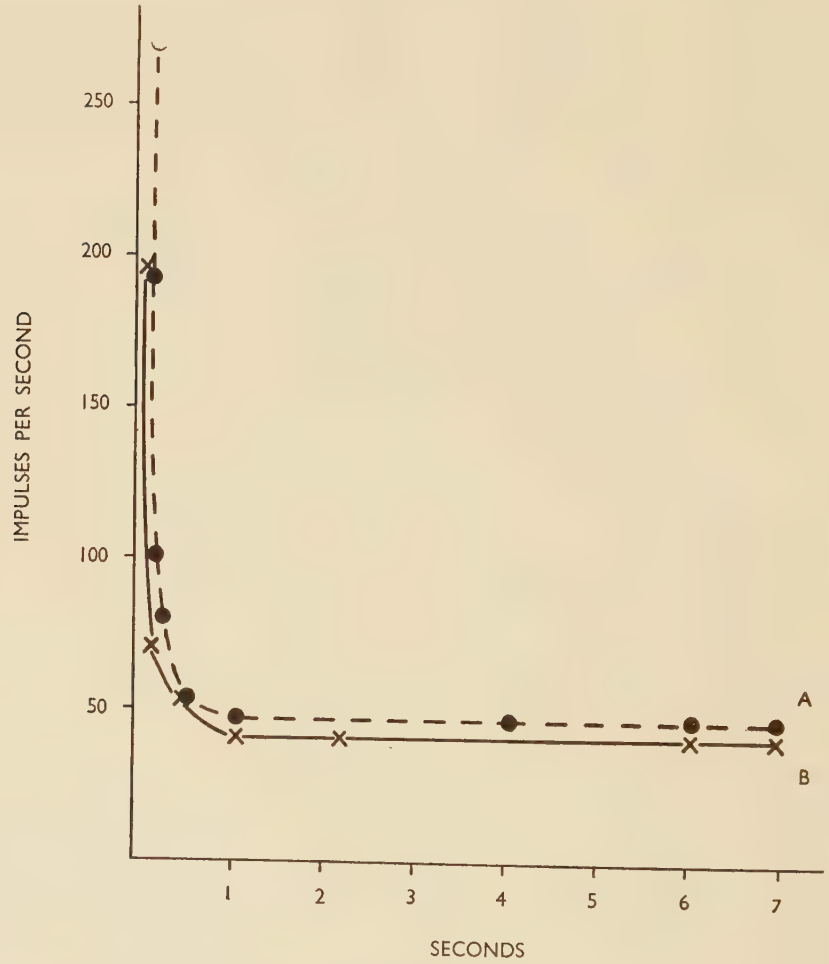


Fig. 5.—Impulse frequency elicited by constant deflexion of single prothoracic hair receptor of *Schistocerca gregaria* plotted against time after onset of stimulus ; curve A resulted from a greater initial deflexion than for B. (By kind permission of the Editors of " Nature ", London.)

Haskell (1959 b) recorded the electrical responses of the prothoracic hairs in relation to bending ; a constant maintained deflexion produced a high

initial discharge rate (Fig. 5) which adapted rather rapidly to a steady level. The response was obtained to deflexion in any direction and the initial frequency depended both on the speed and magnitude of the deflexion ; these responses enable the sensillae to act as motion proprioceptors for head rotations. Attempts at that time to record from the hairs of the cervical plates were unsuccessful owing to the fineness of the fibres and their rapid desiccation after dissection, but recently reasonable recordings have been made by the use of tungsten wire microelectrodes. Even this method only gave a few single fibre records, the remainder indicating that several types of sense organ were carried on the hair plates. Accordingly attention was paid to the anatomy and histology of the hair plates. These are, as mentioned above, situated on the first cervical sclerite, which, with the second cervical sclerite, forms the articulation of the head with the body. The cervical sclerites are key points for attachment of the muscles which rotate the head, no less than five muscles being anchored to the first sclerite and one to the second. The majority of the receptors are concentrated on an oval swelling at the tip of the sclerite, nearest to the postgena of the head (Plate 1, fig. 1). Histological investigation shows that on this swelling there are many hair receptors, characterized by great uniformity of the shape of the hair and reasonable uniformity of length ($97\mu \pm 10$) and with enlarged bases (Plate 1, fig. 2) ; interspersed between them are many campaniform sensillae of the circular, non-orientated type, and a few very small ($20\mu$) tactile hair sensillae ; finally, generally towards the rear of the sclerite, are found some long-haired sensillae with apparently looser articulation.

Responses related to two of these receptors were observed in the electrical recordings, the majority of which showed a predominance of fairly slow, almost non-adapting impulses, subsequently found from single-fibre records to relate to the main hair sensillae. There was no resting discharge present and generally frequency was related to degree of bending, up to impulse rates of about 80 per second (Fig. 6). Increasing movements of the head caused an increase in the total discharge in the whole nerve. Responses to pressure on the hair plate, presumably from campaniform sensillae, were also obtained, with high initial discharge rates and showing incomplete adaptation (Fig. 6). No records relating to the long or very short hair sensillae have been obtained.

The hair organ is surrounded by specialized cuticle of the neck membrane, very thin with a series of pyramidal obtrusions over the surface ; these latter sometimes end in a sharp spike and look superficially like small hair sensillae. This type of cuticle, found also in locust wing articulation, allows bending to occur without transmitting much stress and presumably insulates the campaniform sensillae of the hair organ from cuticular stresses set up by head motion. The hair plates of both sides are partially stimulated in the resting position of the head, while the prothoracic hairs are not. Movement of the head changes the relative stimulation of the plates and excites the prothoracic hairs, so that there is a dynamic sense for head rotations. This system is very similar to that of the Odonata and mantids described by Mittelstaedt (1950, 1952), where four groups of prothoracic hair plates respond to head movement ; Mittelstaedt (personal communication) has recently succeeded in recording

from the nerves of these hair plates in mantids and finds there receptors exactly as in the locust. The main hair receptors give small amplitude non-adapting spikes with impulse frequency proportional to bending ; the hair plates also contain campaniform sensillae and long hair sensillae. In Odonata, Mittelstaedt was able to show that the head, in the light, mediated the dorsal light reaction, while in the dark it was able to act as an inertial stabilizer. The locust mechanism is likely only to operate through the dorsal light reaction, since the head is tightly coupled to the body and is not wide or heavy enough to act as an inertial stabilizer.

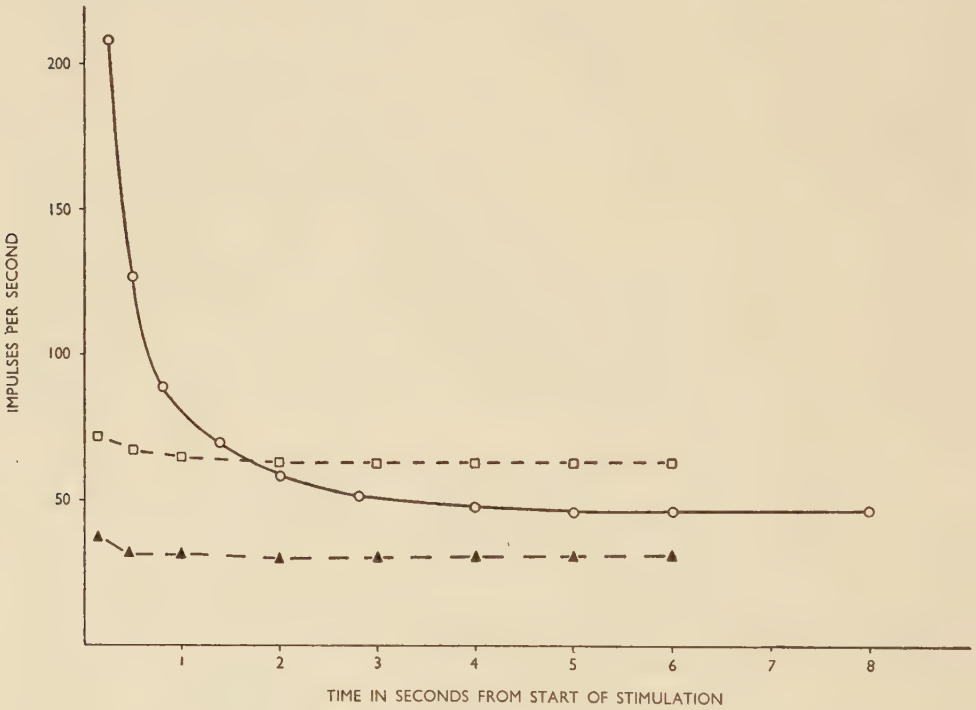


Fig. 6.—Impulse frequency/time curves for certain receptors on the cervical hair plates of *Schistocerca gregaria* ; O—O, receptor sensitive to pressure on the plate (campaniform sensillae) showing high initial discharge and slow incomplete adaptation ; ▲– – –▲, hair receptor sensitive only to bending, showing little adaptation ; □– – –□, same hair receptor with increased degree of bending.

The dorsal light reaction alone is probably inadequate to produce sufficient stability ; furthermore, were it the only mechanism, it would produce very curious flight behaviour as the sun went down, as evidenced by the behaviour of locusts flying in a room with one light on, or caught in a light beam at night. The suggestion derived from field studies of blinded locusts, as mentioned above, is that the compound eyes play a further role in stabilization. Recent electrophysiological studies by Goodman (personal communication) have indicated that the compound eyes of the locust are very sensitive to the rotation of an artificial horizon in front of them, inclinations of as little as 5°

producing a large reponse in the ventral nerve cord. Furthermore, experiments with flying locusts in front of an artificial horizon suggest that this response may play some part in maintaining stability in roll, in conjunction with the cervical hair plates.

After rolling stability, stability in the yawing plane is perhaps most important for locusts, but little is known about possible control mechanisms. However, Weis-Fogh in his original studies on the aerodynamic sense organs of the locust head (1950) found that asymmetrical stimulation of the hair beds by the " relative wind ", that is, the resultant of the wind and air movement due to flight, led to changes in wing motion such as to restore symmetry ; this suggested that the cephalic hairs could stabilize yawing movements during flight, but as Weis-Fogh pointed out, it is very difficult to design wind-tunnel experiments to show this. It is important first to obtain further information on the mode of action of these hairs and recent work by Haskell (unpublished data) has cleared up some points about their structure and physiology and about the nervous pathways associated with them. These details of physiology are irrelevant here, the points of importance being that the hairs can act as an air-speed indicator and that they are directional in action. Laboratory work confirms that asymmetrical stimulation of the cephalic hairs leads to variable oscillations of the wings in flying locusts, and if yawing motion is artificially induced by directing jets of air on to either wing of the locust these are quickly corrected ; this power is reduced if the hair beds are covered.

The rôle played by these organs in free flight is hard to determine ; although they may keep the locust orientated to the " relative wind " due to its forward air-speed and thus prevent yawing, they could hardly orientate it into the prevailing wind unless the spatial and temporal structure of this was such as to stimulate the organ. Present knowledge of wind structure (e.g. Giblett, 1932) indicates that this is unlikely. Covering the cephalic hairs, as field experiments in 1955 in Africa showed, does not seem to affect straightforward flight ; no evidence was then obtained of the effect on flight stability or control. But in field experiments this year on the Eritrean coast with fledgling desert locusts, on a sunny day with winds of from 3 to 6 metres/second, individuals flushed or launched by hand generally flew somewhat up-wind, turned down-wind, flew for a few yards losing height, then turned up-wind to land. Locusts showing this behaviour on two subsequent trials had their cephalic hairs covered with vaseline ; on release, eight out of eleven of these treated locusts moved down-wind losing height as before but failed to turn up-wind to land and made what appeared to be a crash landing. In a second trial with seven of these eight recaptured, only one turned up into wind on landing, the others crashing as before. The take-off of the treated insects was not invariably up-wind, although, as pointed out above, when on the ground the locust has sense organs other than the cephalic hairs with which to orientate to the wind. These few observations suggest that in some circumstances the cephalic hairs can assist orientation, as opposed to stability, to wind, perhaps here in conjunction with optomotor reactions. However, Rainey has also pointed out that these results could be interpreted as showing a loss of ability to make accurate turns consequent on occlusion of the cephalic hairs. This

may also be the case when wind speed increases to or above maximum flying speed when a change of course is needed in order to re-establish " the relative wind ".

Very little is known about the control of pitching in locusts, although Weis-Fogh (1956 a) found that flying was not affected by freedom to pitch about 3 to 4° ; he also found, however, that reduction of the body angle much below 0° resulted in cessation of flight. It is possible that this relation comes into play during gliding, a form of behaviour very often seen in flying swarms ; it is tempting to speculate as to whether Johnston's organ in the antennae may play some part in this mechanism, especially as Hollick (1940) found these receptors played a part in pitch control in flies.

## STRUCTURE OF AND BEHAVIOUR IN SWARMS

Details of the movement of swarms have already been given ; we must now consider the structure of swarms and the behaviour of locusts in them. There are two extremes of swarm formation—the stratiform and the cumuliform. The former type consists of a flat sheet of locusts flying close to the ground, the vertical extent being of the order of 5 to 50 metres. Generally in this type of swarm there are many locusts settled underneath, and progress is with a rolling motion, those at the leading edge constantly coming down to land and the settled locusts at the rear taking off and rejoining the swarm as it moves over. Another feature of this type of swarm is the high volume-density often found—up to 14 locusts/metre$^3$ were recorded in 1945 in Kenya by Gunn *et al.* (1948).

At the opposite pole of swarm formation is the cumuliform swarm, a qualitative description of which is very difficult. These swarms are altogether more diffuse than the stratiform type, with characteristic low volume-densities of the order of 0·001 to 0·1 locusts/m$^3$ and with the locusts extending in the vertical plane from about 100 to more than 1000 metres.

The visual impression of such swarms changes from minute to minute and from hour to hour ; nevertheless, a most general and lasting impression is of groups, sheets, wisps and pillars of rather more concentrated locusts moving, disappearing and reappearing with changing view point. An impression of looseness and diffusion is given, which is belied by objective assessments of the movements and dimensions of the swarm as a whole when it is viewed from aircraft. Such cumuliform swarms also have large numbers of locusts temporarily settled beneath them and progress in the rolling manner mentioned previously. Work by Rainey, Waloff & Sayer (1955) has related the appearance of cumuliform swarms to the presence of vigorous convective turbulence in the air and has demonstrated that many locusts in such swarms could be assisted upwards by up-currents to the level of the isothermal layer which marks the limit of the adiabatic lapse rate from the ground. Rainey & Waloff (1951) cite twenty swarm records, of which twelve were cumuliform and were found in the presence of estimated cloud-base levels of 1,000–2,200 metres above ground, the remaining eight being stratiform, recorded with cloud-base level between 500 and 900 metres.

The size of the swarm also has an effect on structure ; very small swarms of less than 1 sq. Km. in horizontal area have been seen in stratiform formation despite conditions of convective turbulence. Observations on such a swarm of 0·1 $Km^2$ in extent flying about 8–10 metres above the ground made by D. J. McDonald at Garissa, Kenya, in 1956, indicate active behaviour to maintain formation ; a small " dust devil " rose near one edge of the swarm and locusts were carried up to a height of 40–60 metres, but quickly descended, apparently by gliding, back into the swarm as the dust devil subsided. Present data suggest that some minimum size of swarm, thought by Rainey (1958 a) to be perhaps 10 $km^2$, is necessary for full development of cumuliform swarm structure. An additional and most important difference between small, low-flying and generally stratiform swarms and large, high-flying and generally cumuliform swarms is found in their relative rates of displacement with respect to the prevailing wind. The former travel slower than the wind, in the cases examined at never more than 30 per cent of the wind speed ; while the latter travel with the wind at rates between 93 per cent and 108 per cent of its speed (Rainey, 1958 a).

Study of the detailed structure of swarms, mostly made by the technique of double-exposure photography (Sayer, 1956), has shown, as remarked above, that the strong subjective impression of many observers of orientated purposeful flight is a myth. It is, however, true that swarms include groups of locusts, of variable size, all with common orientation within the group ; but the groups constituting a swarm have the greatest possible divergence of orientations, which bear no relation to the direction of displacement of the swarm as a whole. Such behaviour and structure could be expected, on physical grounds, to bring about dispersal of the swarm very quickly ; nevertheless, as explained above, no such phenomenon occurs, but on the contrary great cohesion is observed. In view of the variety of forces at work in a swarm which could be expected to lead to dispersal it must be concluded that some active behaviour on the part of the locust must counteract it. Rainey, Waloff & Sayer, drawing attention to the well-defined edges of swarms—an area, that is, beyond which locust density drops off sharply—pointed out that the observed facts could be explained if locusts or groups of locusts flying over the perimeter turned and moved in again towards the centre (Rainey, Waloff & Sayer, 1955). Subsequently direct field evidence of such an effect was obtained and Waloff (1958) in an analysis of photographic data showed that although the orientations of locusts in the central part of a swarm were of great diversity (Fig. 7) those at the rear and leading edges were all directed towards the centre. Such behaviour must be directed by sensory inputs and with this realisation we approach one of the critical questions of locust biology—the maintenance of gregariousness in relation to locomotor drive.

The existence of locomotor drive needs no proof ; the purpose of it, teleologically speaking, has been adduced at the beginning of this paper. The reasons for it are at present unknown although the evidence available suggests that it is a particular neuro-physiological state influenced by internal—that is, metabolic and hormonal—stimuli. It should perhaps be pointed out that such a drive can and does appear independent of phase in migratory locusts,

as evidenced for example by the flight activity and consequent displacement during certain stages of the life of *solitaria* adults of *Locusta migratoria migratorioides* (Davey, 1959). Kennedy (1951) has discussed at length the conflict between locomotor drive and the tendency to sensory homeostasis in

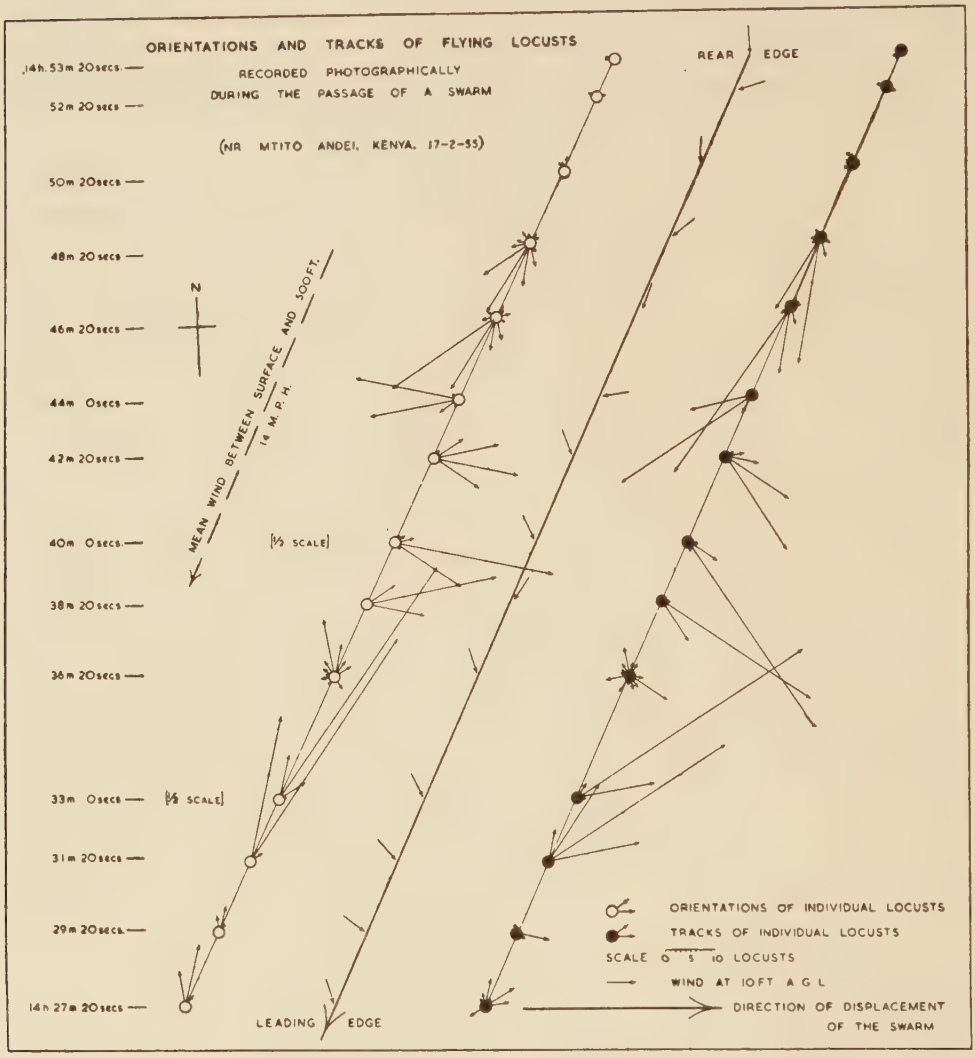


Fig. 7.—Orientations and tracks of locusts in a swarm of *Schistocerca gregaria* obtained from double exposure vertical photographs ; note that orientations at the front and rear edges are predominantly back into the swarm, while those in the centre are very diverse. (By kind permission of Miss Z. Waloff.)

*Schistocerca* and while his argument can still be neither confirmed nor denied it can be extended. The work of Weis-Fogh and Weis-Fogh & Jensen on locust flight has underlined the homeostatic nature of both mechanism and performance and we have discussed previously some sensory mechanisms

relating to this. In the main environment of the migrating locust—the air—there are only two probable sources of disturbing stimuli—the movements of the air itself and other locusts. In the absence of the latter and when disturbances due to the former are not of such a magnitude as to overthrow the homeostatic range of the flight mechanism, it seems probable that locust flight would be orientated steadily up-wind. It would start up-wind because of take-off orientation, it would remain up-wind because of sensory homeostasis. On the assumptions given above that the wind was steady and below the maximum forward flying speed, and in the absence of much convective turbulence, the locust would be flying fairly near the ground ; observations of such flights indicate that the locust climbs so as just to clear any obstacle in its path. Orientation may be provided by a combination of aerodynamic sense organ and optomotor reactions to image direction movement over the retina. The stability of the head, maintained as previously discussed, would assist such flight behaviour. I have personal observations of this type of flight on three separate occasions, and Kennedy (1951) and others report similar observations.

The work of Chapman (1959) on flight in the red locust, *Nomadacris septemfasciata*, is relevant. Locusts in low density tended to orientate and fly upwind and to displace into wind ; at high wind speeds down-wind flight was seen, while the displacement of high-density populations was down-wind. How is this homeostatic flight of single locusts altered by high densities, that is, in swarms ?

As has been remarked above, the two features of the aerial environment which can disturb homeostasis in flight are movements of the air itself and stimuli due to the presence of other locusts ; the presence of the latter may give rise to three types of stimulation which can affect flight—visual, acoustic and mechanical. Olfactory stimulation is of course possible, but the present state of knowledge of locust olfaction (Norris, 1954 ; Loher, 1958) indicates that it only occurs at very close ranges and is in fact chemo-tactile. Furthermore, any such stimulus would be non-directional and the observed behaviour of locusts in swarms appears to involve directional stimuli. Consideration of the swarm structure model proposed by Rainey and his colleagues and the maintenance of cohesion by inward flight at the perimeter requires postulation of an " attractive force " between locusts and groups of locusts ; we need for the moment say nothing about the mechanism of such a force. If this process was the only mechanism acting, all locusts would presently collide in one group ; we must thus also postulate a " repellent force " which comes into play to prevent collision, to allow each locust sufficient room in which to fly properly and to carry out corrective manoeuvres related to stable flight. From observations on actual behaviour of swarms it seems likely that the attractive force operating at the perimeter is effective over fairly long distances ; on the other hand, locusts do fly in high volume densities and hence repulsion probably acts at short distances. At some critical distance the forces balance and this distance should thus be a measure of the preferred distance between locusts in swarms and one they would strive to maintain ; there is, in fact, some suggestion of a " preferred density " of flight in locusts

in a few cases examined, although the limits are wide. The concept is also related to the fact that swarms have well-defined edges. It is interesting to consider the hypothesis further in the light of what sense organs are available for the mechanism suggested.

Three types of stimulus are involved—visual, acoustic and mechanical, the last being the turbulent wake of a flying locust, suggested by Mason (*in* Rainey, 1958 a) ; locusts can perceive such stimuli by means of the compound eyes, tympanal organs and aerodynamic sense organs. What are the probable ranges of action of these stimuli ? To answer this question fully requires a knowledge of the intensity of the stimulus and the sensitivity of the sense organ responsive to it. In the case of compound eyes these parameters are at present unknown ; in the case of the tympanal organ and aerodynamic sense organ they are partly known. As far as vision is concerned it is not yet clear to what visual features of a locust another locust responds ; it may, for example, be shape, colour, rate of movement or a combination of these three. The range will also clearly alter in relation to the environmental light intensity. In connection with this and with the dorsal light stablizing reaction two observations are of interest. Normally in flying swarms falling light intensity apparently leads to cessation of flight, perhaps because stability and cohesion become difficult to maintain ; on the other hand, flights of solitary *Schistocerca* and *Locusta* take place at night. The work of Burtt & Catton (1956) may perhaps be used as an indicator of possible visual range ; on their electrophysiological data of the response of locust ommatidia to movements of a light source of as little as 0·1° of arc, Rainey points out that such an angle is subtended by the body of a locust at about 30 metres. We could thus expect the " attractive force " to operate over distances of this order of magnitude and in fact in the field observed distances over which individuals or bands of locusts flew away from the edge before turning back to the swarm have been up to about 20–25 metres (Haskell, 1957).

A further point about visual stimuli in this connection is related to the recognition by a locust of a fellow locust or the swarm. This can hardly depend upon features like colour or size ; locust colour changes with sexual maturity and swarms of mixed colour occur, and furthermore, sexual dimorphism with striking differences of body size has been observed in swarms of *Schistocerca*. Again, mixed swarms of *Schistocerca* and *Locusta*, species of different size, have been observed on many occasions in coherent flight for some days (Trochain, 1931 ; Golding, 1931, unpublished data). However, what these species have in common is the range of their wing-beat frequency. This parameter is one of the most constant features of locust flight, as pointed out by Weis-Fogh (1956 a, b) even being independent of large changes of temperature. Now the frequencies in question, 17–20 cycles per second, are well below the flicker fusion frequency of locust compound eyes which is of the order of 30–36 c/s ; they might therefore be perceived by the insect and perhaps act as a " recognition signal ".

As far as the mechanism of the " attractive force " is concerned, several possible mechanisms of action can be considered. It is simplest to imagine that the relative degree of stimulation of the compound eyes by the " recogni-

tion signal " leads to turning towards the most stimulated side. The present known distribution in the locust central nervous system of signals related to optic stimuli (Burtt & Catton, 1956, 1959 ; Satija, 1957) is quite compatible with this idea. The known visual field of the locust (Whittington, personal communication) is such that passage over the edge of a swarm at any angle other than perpendicular to that edge must result in asymmetric stimulation of the compound eyes and hence initiate turning movements ; the actual direction of turning is of course immaterial. If a group of locusts flew over the edge, the turning reaction of the leaders could result in turning of the group through the mechanism of gregarious re-alignment (Kennedy, 1951). It is perhaps significant in this respect that the angles subtended by ommatidia of *Schistocerca* in the horizontal plane of the compound eye are about three times those subtended in the vertical ; this means that summation time for perception of horizontal movement stimuli will be prolonged, successive images will less rapidly fuse and the capacity for discrimination will be greater than in the vertical plane.

While such a mechanism could operate as regards horizontal flight and movements, it is a little more difficult when one considers vertical movement, which occurs frequently in large swarms due to convective turbulence. There is no indication that locusts have any altimeter or have a preferred height of flight although in calm conditions flight is generally confined to 100 metres or less above the ground, when visual signals may give the necessary information on vertical movements. The whole question of regulation of vertical movement is a difficult one ; it has been observed (see above for a detailed case) that locusts lifted above the main body of a swarm by thermal up-currents return to it by gliding, although in this case the height of flight was low and visual signals could probably have operated. The mechanism of cessation of flight and initiation of gliding is unknown ; it cannot easily be attributed to diminution of free lift as the thermal slows down, a change which might be detected by the lift-sensitive system postulated by Weis-Fogh (1956 b), since gliding is often observed at quite low heights when locusts at the front edge of a rolling swarm come down to land. It has been suggested that the tympanal organ of the locust might respond to air pressure changes related to vertical movement (Rainey & Waloff, 1951) but Pumphrey (unpublished) could detect no change in nervous response of the organ on stimulation by changes of pressure equal to vertical displacements of the order of 80,000 ft/min. These experiments were criticized (Rainey & Waloff, 1951) on the ground that the rate of displacement was in excess of that experienced by a locust in nature and may hence have obscured any response. Haskell (unpublished data) has recently repeated them using rates of change of pressure equivalent to rates of uplift actually experienced by locusts in the field, but with the same negative result as Pumphrey ; the only effect that might be of significance was that after several minutes at pressures equivalent to heights of 2000 metres the rate of spontaneous discharge from the organ was reduced, but changes of pressure had no effect. Rainey (1958 a) quotes evidence to show that it is unlikely that locusts deliberately utilize up-currents to gain height. The problem of vertical movements and their regulation still requires attention.

We must now consider the remaining stimuli likely to be set up by a flying locust and detectable by its fellows in a swarm ; these are acoustic and mechanical stimuli. Acoustic stimuli and their detection have been investigated by Haskell (1957) in relation to the flight of *Schistocerca* in swarms. Single locusts during flight produced a noise synchronous with the wing beat, with an average acoustic power of about 7·2 ergs per second and with a frequency spectrum from 0·064 to 6·4 kc/s ; 70 per cent of the total energy was radiated in the band 3·2–5 kc/s and measurement of the average threshold for the tympanal organ over this frequency band gave an acoustic range of about 2–3 metres. Recordings and analysis of the noise of swarms were also made and this had a frequency spectrum similar to random noise but of restricted and rather high frequency range. The range of 2–3 metres over which one locust in a swarm could hear the wing beats of its neighbour is of the right order of magnitude for repulsion. Behaviour tests on deafened locusts during the original work showed no abnormality of flight but this was not expected ; it is impossible to follow the behaviour of any one given locust in a swarm so as to observe its reactions to its neighbours. Recent experiments in the laboratory with two flying locusts have shown some tendency for them to take avoiding action—shown by wing twisting—when brought to within about a metre of each other with a screen between. When the tympanal organ of one was punctured, it remained in steady flight even when the other locust was put 25 cms away. However, with other locusts no effect of this sort has been seen and the conditions are very artificial.

Haskell (1957) has pointed out that the general noise of the swarm would certainly stimulate a flying locust's tympanal organ but that since the noise had no modulation structure it could not produce any characteristic discharge in the afferent nerve and moreover would reduce the chance of a locust hearing the individual " wing-beat " noise of its neighbour and discriminating between changes of intensity as the distance between them varied. However, recent work by Horridge (1960) on central representation of acoustic stimuli in the locust ventral nerve cord indicates that when the tympanal organ is presented with a steady background noise and superimposed pulsed stimuli, it accommodates to the former and intensity discrimination improves ; this mechanism may therefore improve the use of wing-beat noise in flight behaviour and further work to clear this up is now required. Haskell also queried whether acoustic stimuli could aid visual stimuli in the inward flight reaction at the perimeter of the swarm ; this still seems doubtful because of the question of range and as explained above visual stimulation would seem adequate.

The second type of repulsion stimulus set up by a flying locust which could be detected by its fellows is the turbulent wake. Mason, in suggesting this (*in* Rainey, 1958 a) gave as a reasonable figure a wake length of 25 cms, apparently based on consideration of locust body length and flying speed. Experiments to determine the distribution and energy of wake from a flying locust have recently been carried out by Haskell but it is very difficult to know what instrumental data obtained from a locust in tethered flight will mean in free flying conditions. If there is any repulsion between locusts because of wake turbulence it will almost certainly be detected by the aerodynamic sense

organ of the recipient locust and a more promising approach has been to use electrophysiological responses of this hair organ as a wake detector ; using this method, there has been some indication of wake detection over distances up to 40 cms at wind speeds of 2m/s. Again, using two locusts flying one behind the other in a wind tunnel some indication of turning away by the second, lower locust has been observed at distances of about 50–60 cms.

While the evidence set out above is very incomplete it does to some extent uphold the hypothesis that the stimuli discussed may be utilized to space out flying locusts from each other. The ranges of the effects are consonant with the densities observed in swarms. The maintenance of common orientation is discussed by Kennedy (1951) and is probably due to optomotor reactions operating to stabilize the sensory inputs of the " neighbour-image " type ; unfortunately no specific experiments on the rôle of optomotor reactions of flying locusts in relation to station keeping have been carried out and what little information is available (Wootton & Sawyer, 1953, unpublished report) is very confusing, locusts reacting in many different ways to quite simple stimuli. There is clearly a need for work on this aspect of the problem. The rôle of visual optomotor reactions in gregarious alignment and orientation has already been adequately discussed by Kennedy (1951) and need not be repeated here.

By the methods just discussed the maintenance of common orientation in a group of locusts may be achieved, but another question is how such groups are first formed. The suggestion supported by most evidence is that they are formed at take-off ; in general, take-off is into wind, the locust orientating on the ground by means of the aerodynamic sense-organ, and hence common orientation is obtained at the outset of flight. It is apparent that many factors are involved in stimulating take-off, many of which have been discussed by Haskell (1957) ; it is a matter of common observation that locusts, even in a heavily settled swarm, take off in groups and the exact combination of stimuli producing this effect is not known. Recently Chapman (1959) produced data on take-off in the red locust which indicate that the rapid increase in body temperature, about 1° C. in 1–2 minutes, following a lull in the wind may be an important stimulus. Kennedy (1951) and others report take-off in the desert locust, following lulls in the wind ; flight in such conditions could be expected to be steady straight-line flight with the take-off orientation stabilized and maintained. A group with common orientation may thus become airborne ; the distances between locusts and their relative stations would be set and maintained as discussed above and the desirable sensory homeostasis so brought about would be maintained both by the reactions referred to and that regularity which is such a feature of locust flight. Disturbance of this pattern could be due to three main causes : flying beyond the edge of the swarm ; meeting another group of locusts with cross orientation ; movements of the air—e.g. thermal up currents—changing the flight regime. The first of these has been discussed. As to the second, observations on convergence of both small streams and whole swarms have been made and resulted in what Kennedy called " gregarious re-alignment ". One or other of the two converging streams, perhaps because it is smaller or travelling more slowly, re-

aligns itself with the other groups and both now proceed as a whole (Kennedy, 1951). It will of course be asked why this process does not continue until the whole swarm is commonly orientated ; several factors preclude this occurrence. One is that in all manoeuvres some locusts are lost from the group and fly at random, as it were, before attaching themselves at some later stage to another group. There is thus a constant flux of locusts in the air, apart from the orientated groups, as is well illustrated by vertical swarm photographs. Then the effects of air turbulence detach locusts from the orientated groups, or in the case of severe turbulence may even temporarily destroy the coherence of the group. Thirdly, there is the phenomenon of constant settling of locusts under a swarm, with consequent destruction of old groups and re-formation of new ones on subsequent take-off.

This appearance and disappearance of locust groups within a swarm may be related to the different speeds of displacement shown by swarms of different sizes. This may be due to one of two main causes, predominance of up-wind orientation in small swarms, leading to lower ground speeds, or the locusts in small swarms spending less time in flight. Although very little information is available for assessment of the relative proportions of up-wind orientation between small and large swarms, what there is suggests there is little difference between them. On the other hand, heavy settling has been noticed under small swarms and locusts in them may spend less time in the air than those in large swarms. In rolling swarm movement, locusts at the leading edge come down to land and later fly off to rejoin the swarm ; in small swarms the cycle of landing-flight-landing will tend to be repeated quicker than in large swarms because of the smaller linear dimensions of the former. It has also been suggested that locusts in large swarms will, simply because they are with more of their fellows, be more stimulated than those in small swarms, and hence will fly more. This seems rather unlikely. The limit to this increase in stimulation will be set by the intensity of the total stimulus derived from the surrounding locusts ; this in turn will depend on the number which can fly within range of the recipients' sense organs. This number must be limited; and it seems likely that in all but the smallest swarms this figure is always reached and the locusts are all maximally stimulated. Also in large swarms, the inter-locust distance is often larger than in small swarms, thus leading to a decrease in stimulation. On the other hand, stimulation will also result from environmental conditions and it may be that those in which large cumuliform swarms migrate give rise to greater stimulation of the locusts.

One phase of swarm activity in which mutual stimulation is likely to change markedly is found at take-off ; much time has been expended in attempts to relate mass take-off to one factor of the environment, particularly temperature (see Kennedy, 1951, for discussion). Temperature certainly has a limiting effect on flight (Rainey, Waloff & Burnett, 1957 ; Weis-Fogh, 1956 a) and may in some circumstances have a stimulating effect leading to take-off (Chapman, 1959). But it seems clear from descriptions of take-off behaviour from several authors (e.g. Gunn *et al.*, 1948 ; Kennedy, 1951) that an important factor is the increase in mutual stimulation as more and more locusts take to the air in milling flights round the roosting site ; when all the

locusts are sufficiently excited to stay in the air, then stream-away begins and the swarm moves off. Individual locusts may take-off in response to different stimuli but they only *maintain* their flight when mutual stimulation is sufficient. Haskell (1957) was able to provoke take-off in some but not all locusts in a settled swarm by play-back of wing-beat noise ; other locusts in the swarm required combinations of acoustic and visual stimuli to bring about take-off. Again, the work of Rainey, Waloff & Burnett (1957) on flight behaviour of the red locust in its outbreak area led to the conclusion that the low relative level of flight activity characteristic of that area was related to the reduction of mutual stimulation brought about by the tall dense grass of the habitat.

This question of the combination of sensory factors in locust swarm behaviour and flight stimulation is most important (Haskell 1957) but at the same time raises great difficulties in the experimental approach by the analytical method. It can only be resolved when a great deal more is known about the sensory capabilities of the locust, the manner in which the sensory data are integrated and how the integrated data affect the operation of the locomotor system. The present paper presents a very much over-simplified view of the events relating to swarm movement and structure ; possible sources of stimuli, such as humidity, have not been mentioned and behaviour patterns of potential importance such as the sun compass reaction have been ignored. This has been deliberate because it is felt that greater progress will be made by drawing attention to those sensory modalities which are clearly involved in the story as it is at present understood. As our knowledge of what happens increases our ability to find out how it happens will increase in proportion.

## SUMMARY

1. An outline of the present hypothesis on swarm movements of the desert locust is given and its probable rôle in the biology of the species discussed.

2. The discussion leads to the conclusion that the main sensory demands of locust swarm flight are related to maintenance of steady stable flight and the maintenance of cohesion between locusts.

3. Sensory mechanisms involved in flight stability are discussed. Stability in roll seems to be partly mediated by a dorsal light reaction of the compound eyes together with proprioceptive feed-back from receptors on the cervical hair plates. The structure and physiology of some of these receptors is discussed. Stability in yaw seems dependent on the cephalic hairs and details of experiments relating to their physiology and function are given.

4. The structure of swarms and the behaviour of locusts in them is discussed, with particular attention to observed behaviour leading to cohesion, such as the inward flight of locusts at the perimeter of a swarm. To explain this reaction and the maintenance of preferred inter-locust distance it is postulated that a visual mechanism exists attracting locusts to one another, while acoustic and mechanical stimuli produced by locusts in flight tend to repel other locusts. These attractive and repellent forces normally balance at the " preferred inter-locust distance ".

5. The possible mode of action of the attractive and repellent forces in relation to the receptors that subserve them, namely the compound eyes, the tympanal organs and the cephalic hair organs, is discussed in relation to the data available on the strength of stimuli and sensitivity of the receptors.

6. Group formation and mutual stimulation by locusts is discussed.

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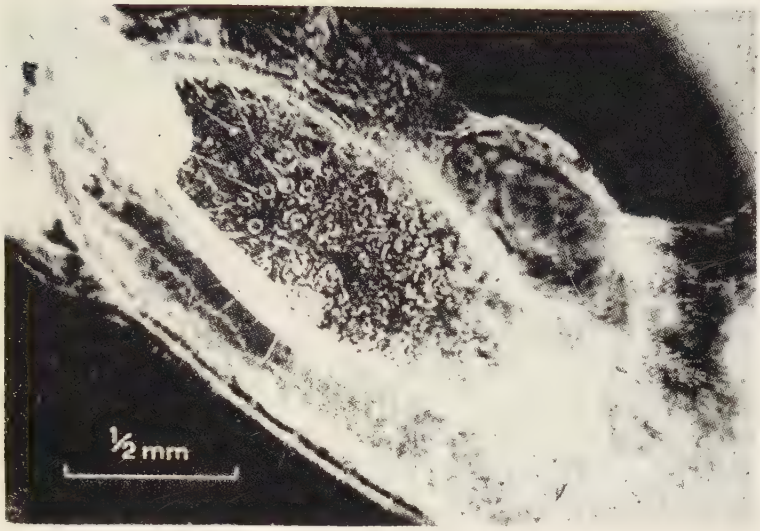


Fig. 1. Photograph of hair plate at tip of first cervical sclerite of *Schistocerca gregaria* showing some of the principal hair sensillae.
(By kind permission of Dr. L. J. Goodman and the Editors of "Nature" London)

Fig. 2. Photomicrograph of principal hair sensillae on cervical hair plate; note rather uniform shape and length of hairs.

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# THE SENSORY EQUIPMENT OF SOCIAL HYMENOPTERA

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Social existence affects perception and offers exceptional opportunities for studies of sensory faculties. Sensory specialization is present as part of wider coadapted changes in response to the environment. This is exemplified by a consideration of ant and bee castes. Some new results are described concerning the colour adaptation of honey bees and their odour discrimination. An electronmicrophotograph of an insect ommatidium is shown, features of which are capable of explaining the perception of the plane of polarized light. A number of sensory faculties is inferred from observed methods of communication, mainly from the dance language. It is suggested that the main effect on the sensory equipment of the social existence of Hymenoptera consists in the incorporation of preexistent sensory elements with motor elements into systems of communication.

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## INTRODUCTION : DEFINITIONS, MATERIAL, APPROACH

A student of sensory specializations in the social Hymenoptera might be interested in specific effects which social existence exerts on sensory equipment ; or he might be simply attracted by the exceptional research opportunities which these insects offer and use them for studying sensory adaptations to non-social factors. Both approaches will be evident in this paper.

The sensory equipment of an insect consists of specific receptors, primary afferent nerve fibres, primary junctions, higher order junctions and fibres and finally specific central cells and connections. To these must be added peripheral ancillary structures such as membranes in tympanal organs or the dioptric and catoptric elements in eyes. All these structures can be studied by morphological techniques and their functions explored either in isolation or in combination by physiological methods.

Finally these structures and functions can be compared in related animals and discussed, taking into account their individual ecology.

There exist some ten thousand species of Hymenoptera—of which several hundred at least are social—each living in its specific habitat and carrying at least twenty different kinds of sense organs. Only a minute fraction of this vast field has been explored but even so the choice of examples has had to be highly selective.

This paper deals mostly with bees, particularly the honey bee, with the behavioural approach predominating. This is not to imply that ants or hornets are less interesting than honey bees or that non-behavioural methods are unimportant.

Traditionally sensory specializations or adaptations have been studied in animals living under extreme physical conditions, for instance in the complete darkness and constant temperature of the deep sea, or in cave animals, and reductions and hypertrophies of individual sense organs are then readily recognized. But in the absence of such obvious cues—both of which incidentally apply to some social insects—we must adopt a somewhat more sophisticated approach looking for rather subtle and at the same time less localized features of specialization. Following an idea formulated by Tinbergen (1959) who called adapted features systems, we shall consider adaptations in the sensory sphere as part of wider coadaptations in the afferent and efferent apparatus. From this point of view we can see the value of great visual acuity of a drone only if it is matched by his subtle manoeuvres during the nuptial flight ; perception of the odour of food, of a colony mate or of an intruding stranger would be quite useless without effective motor faculties to act ; the coadaptation of perceptions and movements during the dances of foraging bees are perhaps the most impressive example.

Within the afferent sphere also the various sense faculties must be coadapted to be useful in any special environment ; visual and chemical faculties operating in the recognition of such natural objects like flowers or prey must be finally adjusted so as not to yield contradictory information. Similarly, within the visual sphere the perception of the azimuth of the sun and the interpretation of the polarization of the sky must also be so coordinated as not to conflict.

Thus we shall not only describe how a few sense organs work but will also discuss how they cooperate and what role they play in the life of their bearers. Finally we shall have to speculate how their special and, to our minds, useful specializations might have developed.

## SENSE ORGANS IN THE SOCIAL CASTES

Perhaps the most striking effects which social organization has had on the sense organs, are some changes which are part of the emergence of castes ; for instance a reduction in the size of the antennae and compound eyes of the asexual forms. This reduction is comparatively minor in the workers of the social bees, which have retained their wings, but is quite pronounced in the ants, where " workers " and " soldiers " are wingless, while the sexual forms at least temporarily have retained their wings. The apterous castes of ants have also completely lost their ocelli (Fig. 1). Lack of wings and the inability to fly on the one hand and lack of ocelli and reduction of compound eyes on the other hand have been shown to be a correlated characteristic (Kalmus 1945) in the whole insect world, separating orders, families, genera and species, as well as phases of the same species of social insects (aphids) and, as shown here, castes. In some families a more graded correlation occurs between ocellar development and wing size. Other sense organs also differ between

castes and sexual forms. How all this came about is quite mysterious. The occurrence of certain mosaics in ants, however, provides us with some information concerning the ontogenesis of these coadaptive structures. Figure 1 shows you the head of a dinergatandromorph in which the right half of the head is " soldier " and the left half male ; the latter being smaller nevertheless carries a large compound eye, a long antenna and ocellar structures, whereas the larger soldier half carries a reduced compound eye, a shorter antenna and no ocelli. We do not know the precise origin of this particular mosaic—it might be the loss of one set of chromosomes in an embryonic cell in the region

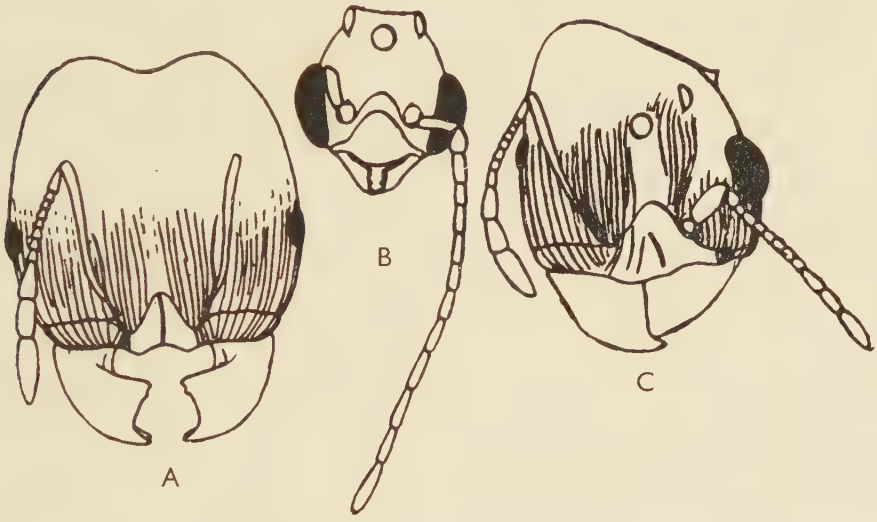


Fig. 1.—Heads of a soldier (A), male (B) and a mosaic dinergatandromorph (C) of *Pheidole pallidula* (from Vandel, 1931).

of the future head, or the fertilization of such a cell after cleavage, but we can be sure that the observed covariation is not the result of a simple gene mutant : eye and ocelli mutants in *Drosophila*, *Ephestia* and many other insects do not affect wing development and wing mutants do not as a rule affect the eyes. Furthermore, bee workers are in no way genetically different from females. Thus we must conclude that selection has perfected systems, capable of producing during embryogenesis several types of individuals exhibiting many and different intricate correlations between their sensory-motor and also sexual activities.

The range of variation of the sense organs in the social Hymenoptera is very great and it roughly parallels the range of ecological conditions. These can be illustrated in respect of the eyes. The sexual forms of social Hymenoptera have, with the exception of certain ant species where the males are wingless, good visual faculties. But as they spend a good deal of their lives inside their dark nests they must be capable of performing various activities without the help of the eyes. The workers and soldiers of many ant species, as well as those of termites, live permanently in the dark even outside their nests and have, as already mentioned, small and poorly developed

eyes. On the other hand the workers of bees and wasps which spend some of their days flying in the open have fully efficient compound eyes and carry ocelli. Hornets which have even bigger eyes can fly in bright moonlight (Blakith, 1955). Thus it seems that complete darkness produces reductions in the visual apparatus, while relative darkness may occasionally be overcome by increased visual efficiency. Actually not much is known concerning the effects on vision of moderate variation in the size of eyes and in the number and size of ommatidia. But it must be such slight variations on which selection works when specialization occurs. Barlow (1952), measuring the eyes of twenty-seven species of Hymenoptera, has, however, shown that visual acuity and sensitivity increase—if rather little—with eye size.

Differences between the castes and sexes also occur in the brains of the social insects. In the honey bee queens have the smallest brain, workers somewhat larger brains and drones the largest. Furthermore, queens have smaller antennal lobes than drones and workers, and the latter show the great internal complications. Parallel to the varying eye size drones have the largest eye lobes and queens the smallest. The pedunculate bodies, which are the coordinating centres for many sensory and motor functions and possibly also the seat of memory, are the longest in the workers (Jonescu, 1909).

## THE SENSORY EQUIPMENT IN THE SERVICE OF THE INDIVIDUAL

The reaction which has probably most contributed to the study of the sensory faculties of honey bees is foraging, that is the collecting of nectar and pollen. Foraging is a social derivative of individual feeding and has a great experimental advantage over it of not stopping when the individual hunger is satisfied. Thus a worker bee may make thousands of flower visits a day and also return several hundred times to its hive. This steady behaviour has been most successfully exploited since v. Frisch's early studies (1915, 1919, 1939) for conditioning bees to a variety of stimuli and later indirectly also for the study of communication (1951).

Several sense organs do normally guide a honey bee to nectar or pollen : the colour, shape and pattern of flowers are perceived by means of the compound eyes ; their odour by antennal organs. Receptors on the proboscis indicate the sweetness of nectar and greatly affect the urge of a forager for returning to a particular site. The volume of ingested nectar is probably perceived by sense organs in the wall of the crop (Kalmus, 1938). Of the many details of visual and chemical perception of bees which we owe to v. Frisch (1915-1950) and his school, a few are relevant to our problem of adaptive organization. Thus Daumer (1956) has summarized the evidence showing that the spectrum of light, visible to bees, is shifted towards the short waves so that they perceive ultraviolet but not red. The same author has shown (1958) that this colour range as well as the particular trichromatic nature of the bee's colour system accord well with the pigmentation of bee-pollinated flowers. He has, for instance, confirmed that some flowers have honey guides, which are invisible to us but visible to bees. But it is a moot point whether the ancestors of present bee-pollinated plants have mainly adapted their petal colour to the possibly restricted faculties of some ancestral bees' colour

perception, or whether perception has been moulded by the arrays of flower-pigments displayed. Both interpretations are possible : some bird-pollinated plants have developed bright red petals or bracts not usually found in species which are pollinated by bees, whereas some Lepidoptera have managed to produce visual pigments sensitive to red light (Ilse 1929).

Whether the social Hymenoptera differ in colour discrimination from their non-social relatives is doubtful ; at present there is no direct evidence for this and it is difficult to see why, for instance, honey guides should be more effective in attracting individual social bees than individual solitary bees ; nevertheless, differences may have developed, information concerning colour is apparently not communicated by one foraging honey bee to another (Ribbands 1953), wasps do not inform each other of the presence of food (Kalmus 1954), and most ant workers have rather poor vision. Thus colour very likely is missing from the " vocabulary " of the social insects, but that does not mean that the faculty of communication need not have an effect on colour vision : it might very well have an adverse effect by favouring olfactory as well as other complex visual faculties at the expense of the colour sense. The same may also apply to the perception of visual patterns, which likewise (unpublished) cannot be communicated by foragers.

I now describe some results which I obtained last summer and which may contribute to our knowledge of the colour adaptation of the Hymenoptera. We know from our own experience that the brightness and colour of an object is perceived relatively to the brightness and colour of its environment. A sheet of white paper in a dim room may reflect much less light than a sheet of dark grey paper in sunshine, but still we do not hesitate to call the first light and the second dark. The colour of an object is likewise computed by simultaneous contrast. This had been common knowledge since 1820, when Goethe published his Farbenlehre, but has been somewhat neglected in the last decades ; recently, however, Gehrke (1948) and Land (1959) have revived these old insights as far as human vision is concerned and have indeed added new and striking demonstrations. Bees visit flowers under greatly variable conditions and illumination and it seemed to me that experiments on them along those lines might be possible. The procedure was as follows (Fig. 2). Bees were trained to a star made from blue paper on a patterned platform, rotating on top of a box in daylight as shown in Fig. 3. When they had learned the colours the coloured star was removed and sodium light was switched on from below. A " grey " star then appeared vividly blue to my eye and the trained bees visited an empty feeder on top of it. Similar results were obtained with other colours and illuminations in conformity with the trichromatic vision of the bee as established by Daumer (1952), demonstrating the fundamental similarity of colour computation in mammal and insect.

The orientation of honey bees to the plane of polarized light is of course well known (v. Frisch, 1948) though mechanisms of orientation to polarized light in general may be quite varied (Kalmus 1959). In this context it is of interest to compare a model* constructed by v. Frisch many years ago, and devised to show how the bees' ommatidia might perceive polarization (Fig. 4)

* The model was demonstrated to the audience.

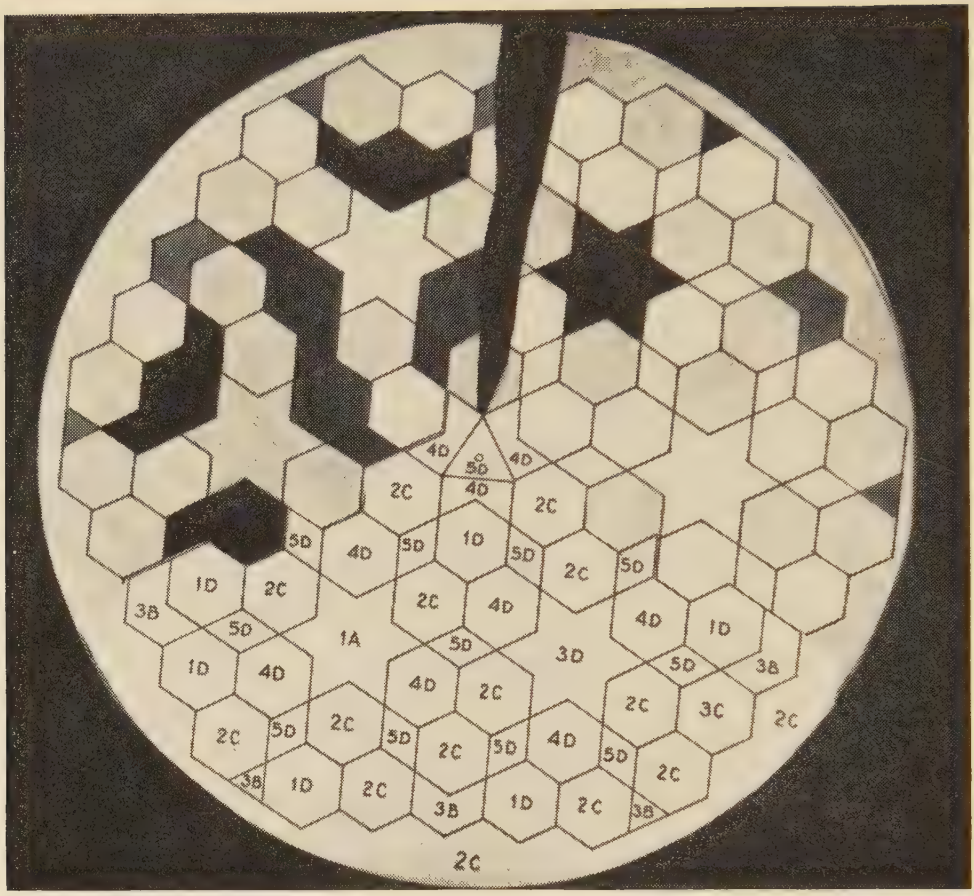


Fig. 2.—Patterned disc for training bees in dual illumination. Shading on the top side (Sector A) reflecting incident light and transmitting light from below ; shading underneath (Sector B) only transmitting light. Sector C shows a numbered grid referring to reflectance and translucence of the pattern elements ; this is not part of the experimental arrangement. The original pattern was demonstrated to the audience, illuminated with daylight from top and sodium light from below, when the element 1A appeared a vivid blue. Other combinations of light sources produce different colours.

with a recent electronmicrophotograph of a transverse section of the rhabdom of an insect (Fig. 5)† (Fernándes & Morán, 1958). The arrangements are very similar showing sectors of differently orientated structures. In the model these are polarized foils and in the eye probably membranes directionally arranged in such a way that the visual pigments rigidly attached to them can serve as directionally sensitive absorbers. It appears that neighbouring and similarly orientated ommatidia in such an eye form a number of systems and this may be the basis for a mechanism serving the perception of polarized sky areas.

† The apposition eyes of honey bees show similarly orientated structures but are difficult to photograph with an electron microscope, therefore a picture of a super-position eye of a moth is shown.

The antennae of bees also carry temperature receptors, though not exclusively ; as there are quite a number of different kinds of receptors on the antennae, we do not quite know which they are. Heran (1952) has been able to train bees by feeding them at particular temperatures and showed that they were accurate to about 2° C. and that this faculty progressively decreased as the distal segments of the antennae were removed. Furthermore, he

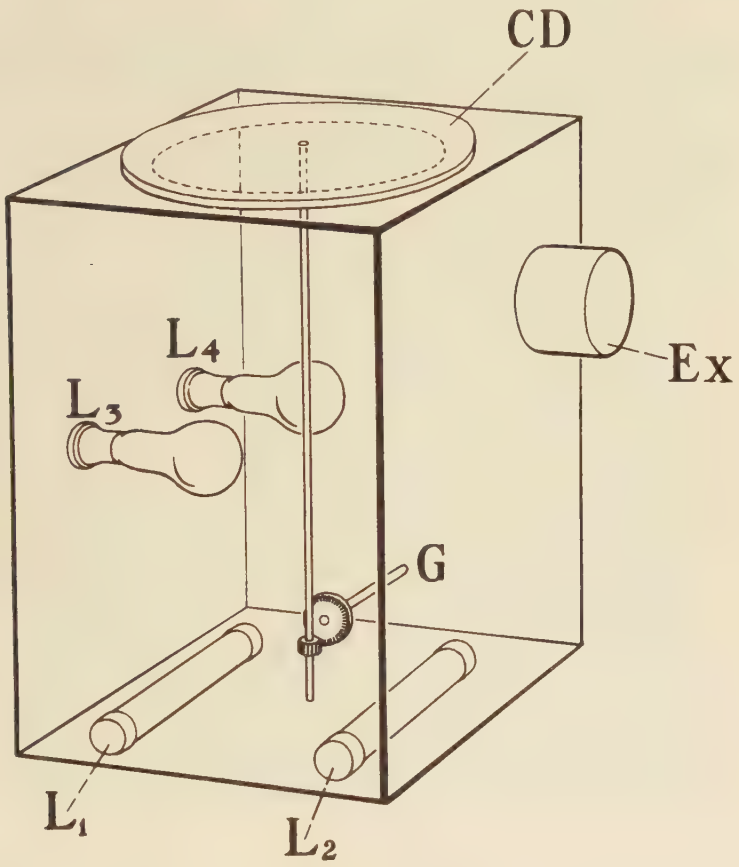


Fig. 3.—Apparatus for turning the patterned disc (CD) once a minute. G = gearing to motor, $L_1$–$L_4$ = various light sources. Ex = exhaust.

showed that bees have a preferential temperature, which varies somewhat with age and with the season. It is safe to assume that these receptors play a rôle in the temperature regulation of honey bee colours, both in winter, when high temperatures are generated in the cluster, and in summer, when water may be collected by numerous carriers and evaporated by others in the neighbourhood of the food chambers.

I cannot here deal extensively with the chemoreceptors on the antennae but can only describe some results which concern olfactory discrimination. Figure 6 shows part of two gas chromatograms of essential oil of Rosemary

coming from two sources and differing in the relative amounts of the volatile and odorous components. The two oils were barely distinguisable to me but bees trained to the one preferred it to the other and vice versa. This shows that olfactory identification must be the result of a quite complex computation, which must be dominated not so much by qualitative chemical differences and absolute thresholds, than by relative stimulation of one way of reception.

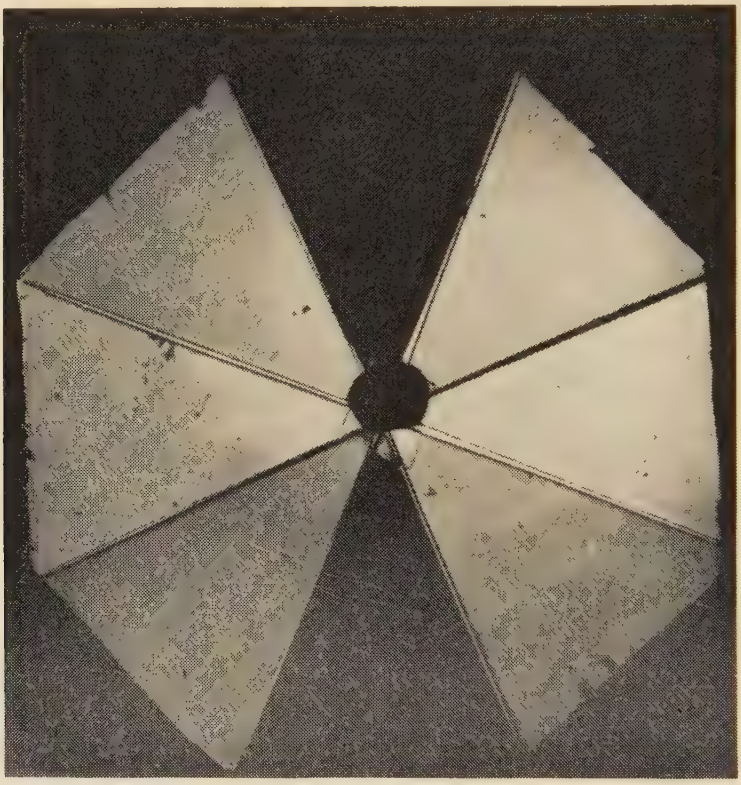

Fig. 4.—v. Frisch's star pattern made from differently orientated triangles of polaroid foil, viewed against a partially polarized light.

The perception of such differences, which is possibly not much bigger than that between the flower odours of varieties of the same species, opens an interesting possibility of investigating a new rôle which pollinating bees may play in the speciation of odorous plants and perhaps also of the effects plant odours exert on the development of odour perception in bees.

## SENSORY FACULTIES INFERRED FROM METHODS OF COMMUNICATION

Let us now consider the rôle of perception in social behaviour and organization. Social organization implies special relationships between some individuals of a species ; members of a particular colony must recognize each other either as individuals or collectively, and they must also recognize

strangers. They must further cooperate and divide their labours. All this depends on communication, and recognition as well as communication are based on the reception and very often the production of signs ("social releasers").

Fig. 5.— Oblique cross-section through a single retinula from the eye of the moth *Erebus* showing the fine structure of the fused rhabdomers (from Fernandes-Moran, *Exp. Cell Research* 1958).

While in principle any of the social responses could be made the basis for studies in perception, in fact, only a few have been useful. The antennae certainly play a considerable rôle in the communication of ants. In bees we are not so sure, but when one worker feeds another, both use their antennae to feel the other's head, probably in order to keep at the right distance and suitably orientated (Butler 1954).

In ants the antennae carry gravity organs, as shown by Vowles (1954). The existence and mode of operation of gravity receptors in honey bees have been recently demonstrated by Lindauer & Nedel (1959). They describe paired organs on the neck and the petiolus, carrying trichoid sensillae, and discuss how the head as well as the abdomen acting as gravity pendulums

affect these organs according to the position of the bee in the gravitational field. Severance of both cervical nerves abolishes geotactic orientation in the dark and the orientation of dancers on the vertical comb, while the unilateral operation has lesser effects. Fixation by glueing of the neck and of the thoraco-abdominal articulation in various positions and combinations also disturbs orientation. The attachment of 50 mg. lead to the back of the head, renders its dorsal half heavier than the ventral half—which is normally the heavier—and transforms the negative geotaxis of a bee into a positive one. These mechanisms may be held responsible for the very accurate gravitational orientation of the combs and cells in the hive and of the dancers in the dark.

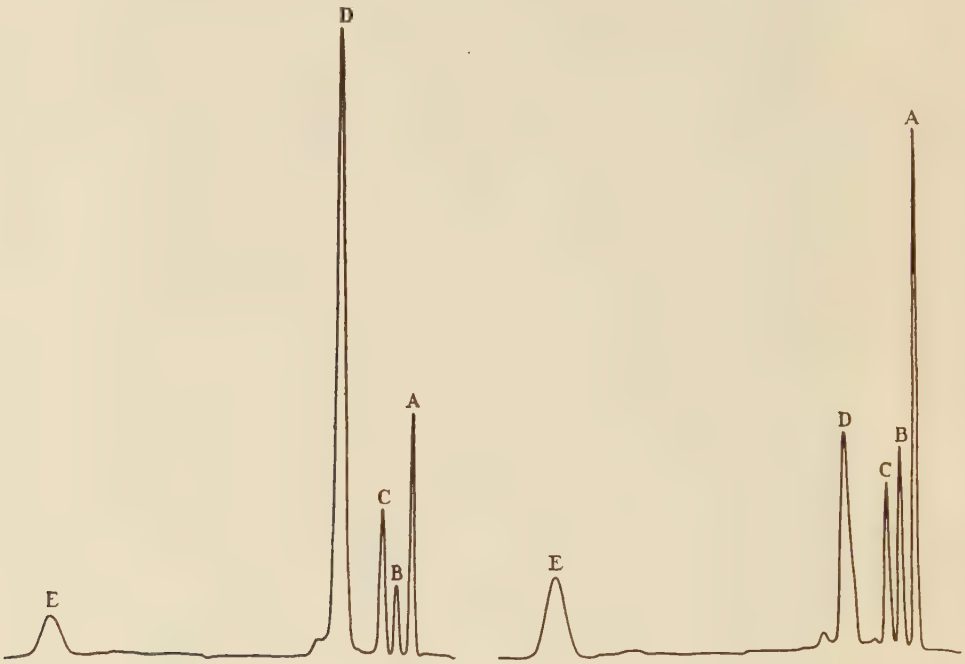


Fig. 6.—Analogous parts of two gas chromatograms of different brands of Rosemary oil, which bees could distinguish, and which also smells slightly differently to the human nose. A, B and C are probably different terpines and one can see that they occur in different proportions in the two samples. There is more cineole (D) but less linalol (E) in the left gas chromatogram than in the right. (Courtesy of Dr D. Holness, Unilever Ltd.)

## PERCEPTION AND COMMUNICATION

The social Hymenoptera as a group are not dominated by any one sense organ. On the other hand, hearing, which plays such an important rôle in the life of many Orthoptera, seems to be on the whole unimportant. There is little doubt that the piping of emergent bee queens—the mechanics of which are still controversial—is perceived and answered by other emergent virgin queens and that this plays some rôle in the process of supersedure (Butler, 1954), but the workers pay little if any attention to these or other

airborne sounds, and we do not know whether they appreciate the rise of pitch in wing beat which we associate with certain situations—e.g. before they sting (Hanson, 1945).

However, worker bees react—usually by some sort of torpor—to solid-transmitted vibrations and have a kind of chordotonal organs in the tibia (Schön, 1911), which seem to be sensitive to these mechanical vibrations ; their sensitivity, however, is less than that of the human ear (Autrum & Schneider, 1948). Similar " subgenual organs " occur in ants and wasps—though we do not know much more concerning the hearing of these groups ; a rudimentary tympanum, lacking in the honey bee, is present in *Lasius* and other ants (Lubbock, 1882). Ribbands (1953) suggests that the subgenual organs—or more likely Johnson's organs situated at the angle of the antennae—might play some rôle in the perception of the " waggling " of a dancing bee, which we shall mention later on. Mechanoreceptors of sorts are numerous on the antennae of all Hymenoptera and probably are alone and in collaboration with chemo-receptors important transmitters of information, but this field is little explored.

The rôle of various—mostly unidentified—sense organs of bees in the service of interindividual recongition and communication can be inferred from the kind of information which one bee can impart to another. Apart from the possible communication by sound mentioned above two groups of means (" languages ") can be easily distinguished, namely a chemical and a behavioural. Among the chemical information is

(1) the composite specific odour of a source of food which is transmitted by the scent of flowers clinging passively to a bee's body (v. Frisch, 1919) ;

(2) the specific odour of every colony, which also clings to the body surface (v. Frisch & Roesch, 1926 ; Kalmus & Ribbands, 1952) and which is also a function of the kind of flowers visited ;

(3) the odour of the abdominal scent glands, which seems to be common to all *Apis mellifica* workers (Renner, 1955) is actively released and which attracts all collecting foragers irrespective of their origin. A scent of this kind—which, however, is produced by the mandibular glands—is responsible for the track marking of certain tropical bees (Lindauer & Kerr, 1958) ;

(4) the queen substance (Butler 1954) produced by the queen and presumably distributed to a majority of workers by licking. Presence of this substance renders a colony " queen right " ; it is probably appreciated by taste.

We now turn to some behavioural means of communication and in particular the characteristic bee " dances ". A returned forager dancing on a comb conveys the following information :

(1) chemical information, i.e. the scent of the visited flowers as mentioned above ;

(2) information concerning the abundance and quality (e.g. nectar concentration) of food ; this is correlated to perseverence of the dancer, i.e. to the duration of dancing (v. Frisch, 1951) ;

(3) information concerning the distance of the food source, or rather concerning the effort needed to reach it. This is correlated to the duration of waggling or the number of waggles during one dance figure (v. Frisch & Tander, 1957) ;

(4) information concerning the geographical direction of the source of food. This is computed from the orientation of the dancing bee on the vertical comb, which is translated into the azimuth of the sun or the polarization pattern of the sky, taking into account the hour of the day (v. Frisch, 1949, 1957).

While the demonstration of these faculties and several others has been most impressive it must be stated that as yet we know very little concerning the mode in which various characteristics of the dance are perceived by the bees, and in fact we frequently do not know which features are the important ones. Thus several observed and correlated features of the waggle dance may in theory convey distance and there may be others as yet unobserved. We can, however, exclude certain possibilities. As the dances are effective in the dark the information normally cannot be visual, and as in an observation hive foragers can be seen to follow a dancer closely and for some time before leaving the hive we may infer that the details of the dance are not perceived from a distance and passively, but that they probably are incorporated first in imitative movements, later perhaps in independent intentional movements and finally direct the actual flight.

It is I think not possible to describe such complex reactions as the product of simple reflexes however numerous. In particular simple afference will not serve as an explanation and we may assume that feed-back information must play a considerable rôle. A bee following a dance must in any case when evaluating the informative features of the dance take into account her own movements ; and it is conceivable that e.g. the quantity from which she infers the distance of an " advertised " crop is in fact not a feature of the dancer's performance but the time or effort which she herself spent in the pursuit of the dancer during consecutive waggling phases. Similarly she may perceive the angle with the vertical of her own body while in pursuit of the dancer rather than that of the pursued. We now know the organs which mediate such information (Lindauer & Nedel 1959), but we can only guess at the rôle which adaptation to social existence may have played in their evolution.

### THE INCORPORATION OF SENSORY MACHINERY INTO SOCIAL BEHAVIOUR

A discussion of this highly speculative problem may start by describing two complex reactions, certainly involving proprioception and occurring in solitary insects, which look like potential preadapted components for communication : Dethier (personal communication) has shown that flies will on occasion ' dance ' near a sugar dish, keeping their movements in a particular plane which is reminiscent of the orientation in bee dances, and Blest (1958) has shown that a saturnid moth (*Automeris aurantiaca*) performs after settling peculiar rocking movements, the number of which is highly correlated to the duration of a previous flight ; this is perhaps analagous to the waggle component

in the dance of bees. Now neither flies or moths are likely to communicate and we can thus assume that these complex behaviour patterns have developed without reference to communication. It is not inconceivable that such patterns have in the course of evolution been *in toto* incorporated in systems of behavioural communication, and that they have been modified later. The whole situation is reminiscent of the evolution of the most important means of human communication, namely of our speech apparatus and our ears. Perhaps the analogy is not too far-fetched if we assume that in the course of the emergence of the social Hymenoptera also pre-existent or if the word, may be allowed, preadapted, sensory organs and faculties have been incorporated into their social communication systems. If this is accepted, central integration of pre-existing functions rather than any great innovation in the structures of peripheral receptors and ancillary structures may be the answer of the hymenopteron to its social environment. However, our factual knowledge is inadequate, the gaps in our understanding glaring, and the whole field is open for enquiry.

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# SENSORY DEGENERATION AND SURVIVAL IN CAVE FISHES

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The present paper attempts to clarify some points of regressive evolution relating to the morphological characteristics and the behaviour of blind cave fishes. The general idea of evolutionary progress in relation to the concept or progressive independence of the organism of its normal environment is discussed. The general problem of regression is defined as a gradual reduction of this biological process of independence. The relationship between regression and abnormality are considered and a description of the biologically abnormal character of regressive faunas and of cave fishes in particular is given, together with some general data on the morphology of the regressed teleostean eye. The survival value of the photic behaviour exhibited by fishes with regressive photoreceptors is discussed and a theoretical interpretation of it is given.

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## INTRODUCTION

Problems concerned with the relations between environmental influences and somatic modifications supposed to be adaptive to special or new biotopic conditions, have always had to face considerable difficulties since Lamarck. When an organism is found to live in a given environment, the very fact of its survival seems to support the idea of a correspondence between the demands of the mesological complex and the responsive capacities of the species considered. Numerous data yielded by psychological as well as physiological investigations show that every organism responds to the surrounding demands according to a general principle of functioning of its receptors. The establishment of an adaptive behaviour cannot therefore be understood without considering finally the significance of certain specific stimuli, whose biological efficiency is always limited to a certain narrow range. This range is what we generally call the normal environment.

The use of this expression calls for careful analysis. It should indeed be realized that, defined that way, the environment is largely a theoretical

concept. Ecology, ethology, experimental studies of sensory functions and mathematical design of behavioural models all converge from different starting-points on the central idea of some average interaction system in which functions are never supposed to exceed the limits of ultrastability characteristic of homeostatic actions. From the point of view of the capacities of sensory equipments in general, all evolutionary processes result with time in some kind of homeostatic equilibrium between stimuli and responses, within the limits of a given set of ecological conditions. It must nevertheless be borne in mind that this equilibrium is never anything but temporary, although it always lasts extremely long on the time-scale of evolution. During the unceasing reciprocal corrections which take place as conditions and morphologies change, mutation pressure on the one hand and selective pressure on the other, oscillate about a mean value, to which the ideal representative of a given species should in principle correspond as much as possible at a certain moment, in its morphology, in its functions, and finally in the integrated behaviour which these make possible.

Such a species would be considered as realizing the best adaptive conditions in a given type of surroundings, and particularly to possess the sensory equipment most liable to convey to it the most useful information for its survival. This we find in the manifold structures of the vertebrate eye for instance, which, from the double-chamber eye of *Anableps* to the bi-foveal eye of birds of prey, seems to have evolved morphological and functional characters generally considered as adaptive. These are not only considered as adaptive, but also as truly progressive in the sense that their lack would greatly reduce the chances of survival of the species considered. It can consequently be said that the idea of evolutionary progress is linked with that of an increase in complexity in the sensory equipment of the animal. For various reasons, a complicated receptor is supposed to prove more efficient than an elementary one. In the case of photoreceptors, it is easy to establish that a light-perceiving organ possessing a dioptric system allowing the accurate focusing of an object, specialized sensory cells ensuring a low reaction threshold and in such number that the power of resolution of the system is high, will prove more efficient to an organism, than undifferentiated pigment-spots randomly scattered on the surface of its body.

The far-reaching distinction of Sherrington (1906) between projicient and non-projicient receptors is based on such an analysis of the sensory functions, and everybody agrees that the evolutionary success of insects and vertebrates, for instance, is largely due to the development of peripheral organs, resulting in the formation of what Sherrington himself calls a precurrent space, not to speak of the corresponding development of functional intelligence. It must, however, be pointed out that the idea of adaptation is very often used on too general a level. The sensory equipment of a given species plays a positive rôle in its survival only within the limits of well-defined ecological conditions. The improvement of the visual function, for instance, can be considered as an evolutionary advantage only in circumstances where long-distance and long-delay responses can currently take place. It may therefore be said that, granted certain ecological conditions, one will be in a position to speak of

evolutionary progress in the realm of the sensory functions of organisms, if any increase in complexity of structure and consequently in efficiency of functioning results in a corresponding increase of the regulatory power of the organism considered, and consequently in increasing independence of its surroundings. This increasing independence appears as one of the main features of evolutionary progress, not only from the point of view of sensory activity, but from the point of view of biology in general (Meyer, 1954).

It is in this sense that sensory specialization may be considered as progressive.

## THE PROBLEM OF REGRESSION

As a consequence of the above analysis it may be said that not every adaptive change is a progressive one. This leads us to consider some special cases of adaptation to peculiar ecological conditions, which everybody agrees to call regressive. Cave biology offers numerous instances of morphological and ethological changes that could hardly be considered as specializations, in spite of the fact that they are truly adaptive in the strictest sense of the word. In a recent study, Heuts (1960) summarized these troglobiotic traits. Confining ourselves to the case of fishes, we may note the following regressive characteristics :

1. *Hypofunction of the body integuments.* This manifests itself in the regression or loss of pigments (guanine) and scales.

2. *Regression or loss of the different parts of the optical system.* This regression affects the various constituents of the peripheral structures, as well as the optic nerve and the optic lobes.

3. *Regression of the endocrine system.* This affects principally the thyroid. Olivereau and Francotte-Henry (1955) have thoroughly studied this particular point on the blind cyprinid *Caecobarbus geertsi*. The hypophysis of the same fish lacks thyrotropic cells and the same gland is very small in the blind Amblyopsidae of North America.

4. *Reduction of the embryological development and of the growth-rate.* Complete embryological development takes between 1·5 and two months in the cave amblyopsid *Amblyopsis spelaeus*, and about three months in the cave brotulids *Lucifuga subterraneus* and *Stygicola dentatus*. The existence of a slow growth-rate has been established by Heuts (1951–1953) on *Caecobarbus* from scale readings.

5. *Low basal metabolic rate*, that of *Caecobarbus* being three to five times lower than that of the epigean *Barbus conchonius*. This characteristic was established by measuring the comparative oxygen consumption of specimens of similar size.

The other typical regressive traits mentioned by Heuts (stenothermy, permanence of neotenic traits), although important are less relevant to our purpose. The regression of the eye structures is dealt with in detail in a further section of this paper.

If evolutionary progress can be defined as a process resulting in an increasing independence of the organism of its surroundings, the various troglobiotic traits just mentioned undoubtedly favour a definition of regression as a process resulting in an increasing dependence of the organism on mesological conditions. This fact has been stressed by various authors who have successfully shown that some definite factors present in the epigean related species, could act as determinants in the constitution of cave populations.

Thus Fage (1931), studying cave spiders could show that defective hygrometric regulation in some epigean species was probably driving these animals towards ecological conditions in which the relatively constant hygrometric level reduced the intervention of regulatory mechanisms. " We are authorized to think," he writes, " that humidity is the main factor in the building up of cave populations and that the cave fauna, so far as spiders are concerned, has evolved on the basis of epigean stocks, whose tissues poorly protected against hygrometric variations in the surroundings, can escape dessication in the moist atmosphere of caves. Their presence in caves remains optional as long as humidity conditions remain sufficient ; this represents the case of troglophils; but it becomes a necessity as soon as their demands cannot be satisfied in their surroundings any more. This represents the case of troglobionts." (1931 : 109) According to the same author, the humidity factor does not only drive the spiders into the cave but it also keeps them definitely in it once they have started inhabiting it. Troglobionts are therefore true " prisoners " of the caves in which they dwell, because any higher variability in the factor considered exceeds the regulatory powers of the species. In other words, the rate of energy exchange proper to subterranean surroundings imposes itself on the organism, which thus abandons a great part of its physiological and behavioural autonomy. In the case of humidity this phenomenon has been called stenhygrobiosis (Fage). Other different instances of the same basic phenomenon are afforded by other organisms adopting cave life.

The most important phenomenon, because the most general on that respect, seems to be the lowering of the basal metabolic rate. As Meyer (1954) points out, the more an organism becomes independent, the more it succeeds, by increasing its regulatory powers, to maintain a rate of energy exchange beyond the level which would be imposed on it by its surroundings. The autonomic temperature level of homoeothermic animals is the clearest instance of this. Lowering of the basal metabolic rate appears therefore as a fundamentally regressive characteristic. In a thorough study of the physiological aspects of regressive evolution in the cave fish *Caecobarbus geertsi* Blgr, Heuts (1951–1953) has succeeded in giving this fact its proper adaptive significance, by incorporating it in a general theory. Like Meyer, Heuts starts from the fundamental antagonism between progressive and regressive evolution, the former being characterized, after Baldwin (1953) as an increase of internal organic stability, the latter being essentially a reduction and ultimately the loss of it. This represents the main feature of subterranean adaptation ; reductions and losses of isolated organs are considered as mere epiphenomena of this basic process. As is well known, any change in the genetic constitution affects the genotype as a whole, including the genetic processes determining

the relations of the organism to its environment. It is therefore not possible to admit that hereditary changes as important as those observed in cave animals, would be physiologically neutral. The caves in which *Caecobarbus* lives (Lower Belgian Congo) are ecologically characterized by intermittent activity in relation with the tropical rain-cycle. From this, the author concludes that food supplies inside the cave must be equally intermittent, and finally that it must exert effects on the growth rate of the fish. This he could ascertain from careful scale readings. Specimens belonging to discontinuous local habitats exhibit great similarities in that respect. These fishes, and probably other species living in similar biotopes, are consequently characterized by an extremely slow growth rate. On the other hand, comparative biometric measurements of the appendages of the cave form *Caecobarbus* and of its nearest epigean relative *Barbus holotaenia*, show that organs with high positive allometry are particularly affected by the reduction of the total growth rate. Among these, eyes and melanophores are the ones displaying the highest positive allometry during the first stages of ontogenic development. It seems therefore easy to understand that they should particularly be affected by the reduction of the total growth rate. This can be considered as the fundamental physiological cause of eye and pigment regression. That the slow growth rate is a typical regressive feature is indirectly confirmed by the fact that, in spite of the irregularities and the scarcity of food supplies, the fishes do not show any external signs of underfeeding. This fits in also with the low level of the basal metabolic rate. Finally, it must be pointed out that the anatomical and functional regression of the thyroid is in complete accordance with this last fact.

The general picture of regression conveyed by these two theories shows from various angles that typical cave dwellers are well adapted to their subterranean biotopes, and that this adaptation is characterized mainly by a lowering of the physiological economy, to which anatomical reductions or losses can indirectly be referred.

## REGRESSION AND ABNORMALITY

Regression, as we have just described it, results from some deep biological necessity. One would nearly be tempted to interpret it as an economical process by which an organism strives to get rid of all the organs becoming biologically useless in certain biotopic conditions, coupled with a simultaneous general lowering of the physiological activity, the latter having only to face very reduced energy demands. One is particularly struck by the general reduction of sensory processes which can be observed in cave animals ; and this again can be easily understood, sensory life being one of the main sources of consumption of organic energy.

This, obviously, is a process of degeneration, in comparison with the morphological and functional characteristics of the epigean species to which cave species are related. Whatever be the causes invoked to explain the presence of regressed fishes in subterranean biotopes, it remains that they represent typical cases of abnormality. Let us consider briefly the reasons in favour of such an interpretation.

1. The taxonomic relations between cave species and related epigean species are based on very close morphological examination. The epigean relatives must therefore be considered as representing the criterion of evolutionary progress at the family level. Consequently, the cave forms appear as typically degenerative. It is nevertheless of interest to the zoologist to remark that in spite of this no systematic study of the blind fishes has up to now gone so far as to identify any blind cave dweller (in the case, of course, of typical troglobionts) with some definite epigean relative ; every known cave fish has received the status of a separate species. Regression is thus considered as affecting the adult morphology to such an extent that the regressive features are considered as endowed, as such, with the value of specific determinants, the other family characteristics remaining mostly unaffected. Thus the blind *Caecobarbus geertsi* is related to the eyed *Barbus holotaenia*; *Trogloglanis pattersoni* to *Ameiurus*; *Pimelodella kronei* to *Pimelodella transitoria* ; *Caecorhamdella brasiliensis* to *Rhamda foina* ; *Anoptichthys jordani*, *Anoptichthys hubbsi* and *Anoptichthys antrobius* to *Astyanax mexicanus*, etc.

2. There exists a definite intrinsic relation between abnormality and regression. If we recall what we have said earlier of the loss of biological autonomy which characterizes regressed forms, we may observe that the phenomenological analysis of behaviour disorders following brain lesions, for instance, leads to similar conclusions. Thus Goldstein (1951 : 40 seq.), studying behaviour patterns of some of his patients, finds that the regulatory powers of the brain are considerably reduced. He observes that the patients try to escape systematically any situation calling for some effort of abstraction. This manifests itself clearly in the fear exhibited by the patients when they perceive disorderly arranged objects or when they perceive empty space. If objects are arranged in disorder on a table, the subject puts them immediately in order ; this makes the situation more concrete and reduces the adaptive demand ; the fear of empty space is typical of aphasic patients ; asked to write on a blank sheet of paper, they will only be able to carry out the order, if they are allowed to draw lines on the paper, and they will then fill the page without leaving any free space between consecutive words. These facts testify of an " extraordinary narrowing of the surroundings in which the patient lives ", and Goldstein concludes : "A deficient organism can only attain an orderly behaviour through a reduction of his surroundings in proportion to the extent of his deficiency." This, of course, is only taken as an instance, and there is no question of comparing directly the behaviour characteristics of brain patients and those of regressed animals ; but the general principle of Goldstein holds true in a broad biological outlook. From the morphological point of view, however, closer studies of the similarities eventually existing between cases of central abnormality and cases of morphological regression would probably prove useful on the theoretical level. Evidence of the reduction of the optic lobes of blind fishes has been given by Stefanelli (1954) for *Anoptichthys jordani*, by Quaghebeur (1957) for *Caecobarbus geertsi*, and by Marshall & Thines (1958) for *Typhlogarra widdowsoni*.

3. Finally, the abnormal character of regressive faunas can be deduced from pure statistical considerations. About forty-five species of typical cave

fishes are known. This represents a truly negligible proportion of the enormous freshwater teleostean fauna. This again pleads in favour of the abnormal character of these species. Deep sea species very often display regressive sensory and pigmentary characteristics, as several oceanographic expeditions have established. But special morphological adaptations, as well as positive characteristics like the presence of light-producing organs, for instance, do not allow us to consider them in bulk as regressive in the same sense as the typical troglobiotic freshwater faunas.

## THE REGRESSED TELEOSTEAN EYE

The regression of the teleostean eye has been investigated by various authors in different species. The results of these studies show clearly :

1. That there exists a relation between the process of eye regression and the general ontogenic development. Larvae of cave fishes generally possess eye structures which are nearly normal in size, and which possess nearly all morphological constituents that are found in epigean larvae taxonomically related to them. As the fish grows, the eye becomes anatomically disorganized and recedes inside the skull. At the adult stage the eye of a typical troglobiotic fish consists only of histological remnants disorderly arranged and completely covered by connective tissue and skin. This process has been thoroughly studied by Kuhn & Kähling (1954) on *Anoptichthys jordani*, and by Quaghebeur (1957) on *Caecobarbus geertsi*.

2. That once completed, the regression varies considerably in extent from one species to the other.

A distinction must be drawn here between cases of simple microphtalmy, where the eye becomes smaller and recedes only slightly inside the skull, and cases of true regression, ranging from slight regression to nearly complete anophtalmy.

A good instance of microphtalmy is afforded by the small Australian brotulid *Dipulus caecus*. As can be seen on the microphotographs (Plate 1), the various histological elements are present and their relative location is orderly ; the eye has merely receded a little and is covered by skin. But this last characteristic is not unfrequently found in many species of fishes. There seems, however, to exist a good differentiation between the corneal and the dermal layer, and the optic nerve is well developed. In the preserved specimens examined, the eye appears from the outside as a bluish spot on the surface of the skin. It is similar in many respects to the eye of *Lampetra planeri* ; in this last instance, too, the eye is histologically normal, but very small and covered by skin (see Walls, 1942 : 451, 452).

Typical instances of regression are afforded by troglobiotic species like *Caecobarbus geertsi* (Quaghebeur, 1957), *Anoptichthys jordani* (Kuhn & Kähling, 1954), *Typhlogarra widdowsoni* (Marshall & Thines, 1958), *Typhlias pearsi* (see Plate 2) and many others. (For a general survey, see Thines, 1955.) In some of these cases the degeneration of the eye structures is so complete that some histological components are either absent or, when present, very difficult to identify.

## THE PHOTOKINETIC BEHAVIOUR OF BLIND FISHES AND ITS BIOLOGICAL SIGNIFICANCE

The extreme regression undergone by the eye of troglobiotic fishes does not allow the formation of differentiated retinal images, at least in the adult forms investigated to the present day. Certain species, however, still display a diffuse light sensitivity, which manifests itself in behaviour under the form of a generally negative photokinesis. Various authors have been able to show that many blind species react at least to very small differences of brightness. (Eigenmann, 1909, on *Amblyopsis spelaeus* ; Breder & Rasquin, 1947 ; Kuhn & Kähling, 1954 ; Lüling, 1954, and Thines, 1954, on *Anoptichthys jordani* ; Thines, 1953 and 1954, on *Caecobarbus geertsi* ; Marshall & Thines, 1958, on *Typhlogarra widdowsoni*.) In certain cases a differential chromatic response has been found (Thines & Kähling, 1957, on *Anoptichthys jordani*).

A supposedly compensatory rôle played by the distant touch and vibratory sense can probably not be substantiated, at least in the case of *Anoptichthys*, since Grobbel & Hahn (1958) have proved that though *Anoptichthys* was more successful in avoiding obstacles than its eyed relative *Hyphessobricon scholzei*, its lateral line system was in no way better developed.

On the other hand, the hypothesis of extraocular light sensitivity localized in the epiphysial region of the diencephalon, calls for serious attention. Owing to the general cutaneous depigmentation of most blind fishes, the pineal area becomes exposed and is liable to be directly stimulated by light-rays (Breder & Rasquin, 1947 and 1950). According to some authors (Eigenmann, 1909 ; Breder & Rasquin, 1947) the biological usefulness of the diffuse light sensitivity found in blind fishes is obvious when the sign of the reaction is negative, i.e. when the animal is photophobic. The possession of a normal teleostean dioptric system can be considered as useless in an underground biotope which is perpetually obscure, whereas the photonegative response can prove biologically useful in principle, by giving to the cave dwellers information on the limits of the biotope, beyond which selective pressure should theoretically lead to the extinction of their species.

It seems necessary to analyze this interpretation in connection with the well-established facts of photic sensitivity of these peculiar faunas. Two hypotheses can be formulated in trying to grasp the most probable significance of the observed photokinetic responses : the hypothesis of remanence, and that of vicariousness.

### *The hypothesis of remanence*

By remanence, we must understand, in the present case, the continuation, in eyeless cave fishes, of the photokinetic functions preexisting in the epigean species from which they proceed. As we have already pointed out, cave life entails extreme morphological as well as physiological transformations, namely at the sensory and consequently at the behavioural level. The main reasons in favour of an interpretation of the photokinetic function of blind fishes as a behavioural remanence, are, briefly, the following : As is well known, eyed fishes display, in addition to their organized visual perception (Herter, 1953), various phototactic and photokinetic reactions. Visual perception in the

proper sense disappears completely in blind fishes, as a consequence of the morphological degeneration of photoreceptors. Phototactic and photokinetic responses appear consequently as the only forms of photic behaviour still available. It may therefore be said generally that photokinesis, the secondary epigean mechanism, becomes the primary subterranean mechanism.

Along the same line of thought Wickler (1957) supposes that photokinetic responses observed in blind fishes are not absolutely new specific forms of behaviour and that they do not develop as a function of the mesological demands proper to the underground habitat, but rather that they exist in morphologically normal forms as latent potentialities, liable to be displayed as soon as the dominant optical orientation happens to fail.

Inasmuch as the photokinetic response still partly depends on the existence of ocular remnants, as Breder & Rasquin (1947) could establish it for *Anoptichthys*, it is endowed with a typically vestigial character, and it can be said that the observed reactions are remanent or residual in this, that their occurrence depends partly on the existence of a vestigial anatomical structure. Therefore, from the point of view of the kinship between cave and epigean species, as well as from the point of view of ontogenic development, the hypothesis of the remanent character of photokinesis seems acceptable.

Two aspects may be distinguished in these vestigial forms of behaviour : (1) A progressive aspect, represented by the prevalence of photokinesis over differentiated vision, the latter having become impossible through the regression of photoreceptors. The photokinetic behaviour is indeed a remanent one, because it is the continuation in a cave species of a function which existed previously in its epigean ancestor, but though remanent it is progressive because its rôle, secondary in the epigean species, becomes prevalent in the cave species. (2) A regressive aspect, represented by the relative dependance of the response on vestigial ocular structures.

The postulated biological usefulness of photokinesis is only conceivable, in principle, if it is considered progressive in the sense just defined.

### *The hypothesis of vicariousness*

One speaks of vicariousness in physiology, when an organ supplants another which has become functionally insufficient. Breder & Rasquin (1950) have shown the rôle played by the pineal gland in governing photokinesis in numerous epigean fishes, the reaction being the more positive as the morphological exposure of the epiphysial area increases. In cave fishes the exposure of the epiphysial zone is generally favoured by cutaneous depigmentation. As the ocular structures of these species become functionless, the intervention of pineal photosensitivity appears as a vicarious function, in reverse correlation with the anatomico-physiological degeneration of the eye. This extra-ocular photosensitivity, well established in *Anoptichthys* (Breder & Rasquin, 1947) will, however, have to be investigated in other cave species before its general evolutionary significance can be fully understood. The fact that pineal exposure is nearly always associated with positive photokinesis raises, however, a basic difficulty with regard to the postulated biological usefulness of photic

reactions of blind fishes, as no reaction of that sign can contribute in any way to maintain the animals inside a subterranean biotope.

Nevertheless, other investigations already quoted at the beginning of this section have furnished evidence of definite negative photokineses in other cave species, whose pineal area is at least as exposed as that of *Anoptichthys*. Moreover, photokinesis is not the only form of behaviour to be considered, and a careful study of the whole behaviour of blind species would probably show that there exist conflicts between the various kineses and taxes present in a given species. The final problem to be faced by the biologist in this perspective would be to ascertain that the result of these interactions determines the choice of a praeferendum endowed with a positive survival value. If we had definite proof that the pineal photosensitivity of epigean fishes is the main physiological correlate of their negative photokinesis, the latter would have to be considered, in cave species, as a progressive remanent function in the sense defined above. Vicarious function and progressive remanent function can therefore be considered synonymous.

In brief, the photokinetic behaviour of blind fishes can give rise to the following interpretations :

1. If this photokinesis is exclusively dependant on ocular remnants, it is only a vestigial form of behaviour and it represents a case of pure or regressive remanence. There is, in this case, a mere continuation at a lower degree of a preexisting function.

2. If it depends exclusively on the photosensitivity of the pineal area it must be considered as a case of progressive remanence ; there exists in other words, a continuation of a preexisting function, but the latter gains in importance in the total behaviour of the cave species because it has become the only reaction mechanism informing the animal of the presence of photic stimuli in the environment.

3. It seems legitimate, for this last reason, to consider that the photokinesis exhibited in these conditions is also a vicarious function, whose localization would be the epiphysial area. The pineal organ would therefore have to be considered in the case of blind fishes, as the vicarious organ of the degenerated eye.

4. Progressive residual or vicarious photokinesis is the only type of photic behaviour to which any survival value can be ascribed, regressive residual photokinesis being necessarily on the way of complete disappearance, like its morphological visual substrate.

These considerations tend to show that the negative photokinesis of cave fishes does not imply necessarily, by its mere existence, the biological usefulness with which certain authors endow it (Eigenmann, 1909 ; Breder & Rasquin, 1947). This biological value is clearly linked with the anatomical localization of the photosensitivity, a point on which electrophysiological investigations will soon, we hope, enable us to throw more light. The existence of a negative sign and of a vicarious localization appear consequently as indissolubly connected. Considered separately, these two factors do not permit any conclusion as to the rôle they may eventually assume in the survival of anophtalmic species.

*Other difficulties*

Other observational facts show also that the biological significance of negative photokinesis in blind fishes cannot be admitted unreservedly. First it should be noted that the photonegative response shows a very high inter- and intra-individual variability as well as high inter-specific variability. The mean percentages of time spent in the dark zone of a simple-choice apparatus, range from 68 to 96 for *Caecobarbus*, from 59 to 70 for *Anoptichthys* and from 50 to 63 only for *Typhlogarra* (Thines, 1954 ; Marshall & Thines, 1958). If these values are interpreted from the point of view of the hypothesis of the biological usefulness of negative photokinesis, as the survival rate of the species considered (the representative value of the samples used being taken into account), its extreme statistical limits range from nearly absolute certainty (96) to mere chance (50). Secondly, these laboratory results only make sense if they are interpreted in their ecological context. From this last point of view two important facts must be considered :

1. Granted that negative photokinesis has a positive biological effect, it must needs exhibit itself in conditions allowing the animals effectively to react differentially to photic stimulation and particularly to brightness. These conditions are only realised in biotopes where there exists a brightness gradient at the entrance of the cave occupied by the troglobionts. Now, hydrographic systems in which blind fishes are found are far from presenting uniform ecological conditions in that respect. Brightness gradients exist at the entrances of the caves inhabited by *Anoptichthys* (Breder & Rasquin, 1947) and by *Caecobarbus* (Heuts & Leleup, 1954), but species like *Uegitglanis zammaranoi* (Thines, 1958 a) and *Phreatobius cisternarum* (Goeldi, 1904–1905) and many others, live in biotopes without epigean zone. Moreover, predatory trogloxens can eventually venture into the dark zone of the habitat, as Heuts & Leleup (1954) have established it for certain blindfish caves of Belgian Congo. For quite a number of cave fishes, therefore, the problem of the survival value of negative photokinesis seems to be difficult to solve.

2. In addition to this, larvae of blind fishes seem to be light-indifferent. This we have been able to establish on young *Caecobarbus* dwelling at the entrance of the Kavuaya cave (Belgian Congo) (Thines, 1958 b), and Kähling (1957) finds the same in his light-conditioning experiments on young *Anoptichthys*. As we have already pointed out (Thines, 1958 b), it is remarkable that a supposedly biologically positive behaviour should fail precisely when it would prove the most useful.

## CONCLUSION

We have tried, in this short analysis, to show the relations between behaviour and morphological characteristics in the realm of regressive evolution. We think it necessary to stress the dangers of interpretations based on the superficial bringing together of data which, though well established in the respective fields to which they pertain, may not allow some very tempting evolutionary conclusions. This is very much the case for the survival value

attributed to the diffuse light sensitivity of troglobiotic fishes, when it is not duly replaced in its proper morphological and ecological context.

To conclude, in accordance with the general theme of this symposium, it may be said that sensory changes occurring in connection with definite environmental demands, may very well be considered as adaptive, but should not be automatically considered as positive evolutionary characteristics. In that sense, it is perhaps legitimate to think that the facts of regressive evolution are liable to contribute in their own way, to a better understanding of the evolutionary significance of sensory specialization.

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## EXPLANATION OF PLATES

### PLATE 1.

A—Transverse section through the head of *Dipulus caecus* (Total length : 93 mm.). The specimen used is probably not adult, as the total length of the holotype given by Waite (Notes on fishes from Western Australia, Rec. Austr. Mus.6, part 2 : 77–79, 1905) is 152 mm. The eyes can be seen on both sides of the head. The section shows successively the dermal layer, the sclerotic tissue, the chorioidal tissue (in black), the successive layers of the retina and the posterior chamber. (× 15)

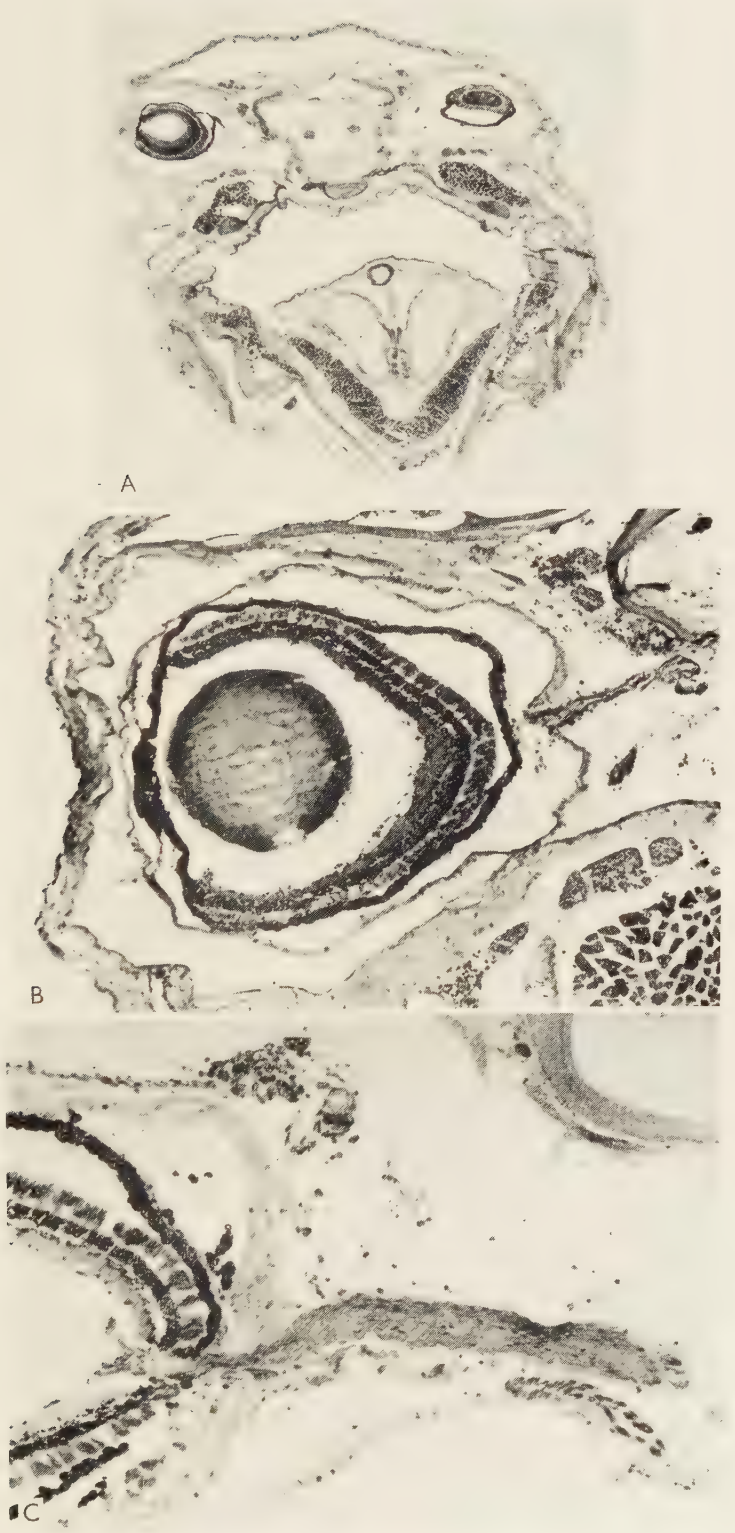
B—Transverse section in the central vertical plane of the eye of *Dipulus caecus* showing successively the dermal layer, the corneal layer, the anterior chamber, some irideal tissue and the well-developed lens. Posterior chamber, retinal and chorioidal tissues as in upper microphotograph (A). The tract of the optic nerve can be seen posteriorly from the level of the sclera. (× 75)

C—Detailed posterior view of the eye of *Dipulus caecus* showing the optic nerve tract leaving the upper plexiform layer and crossing the retinal layers, the chorioid and the sclera. (× 94)

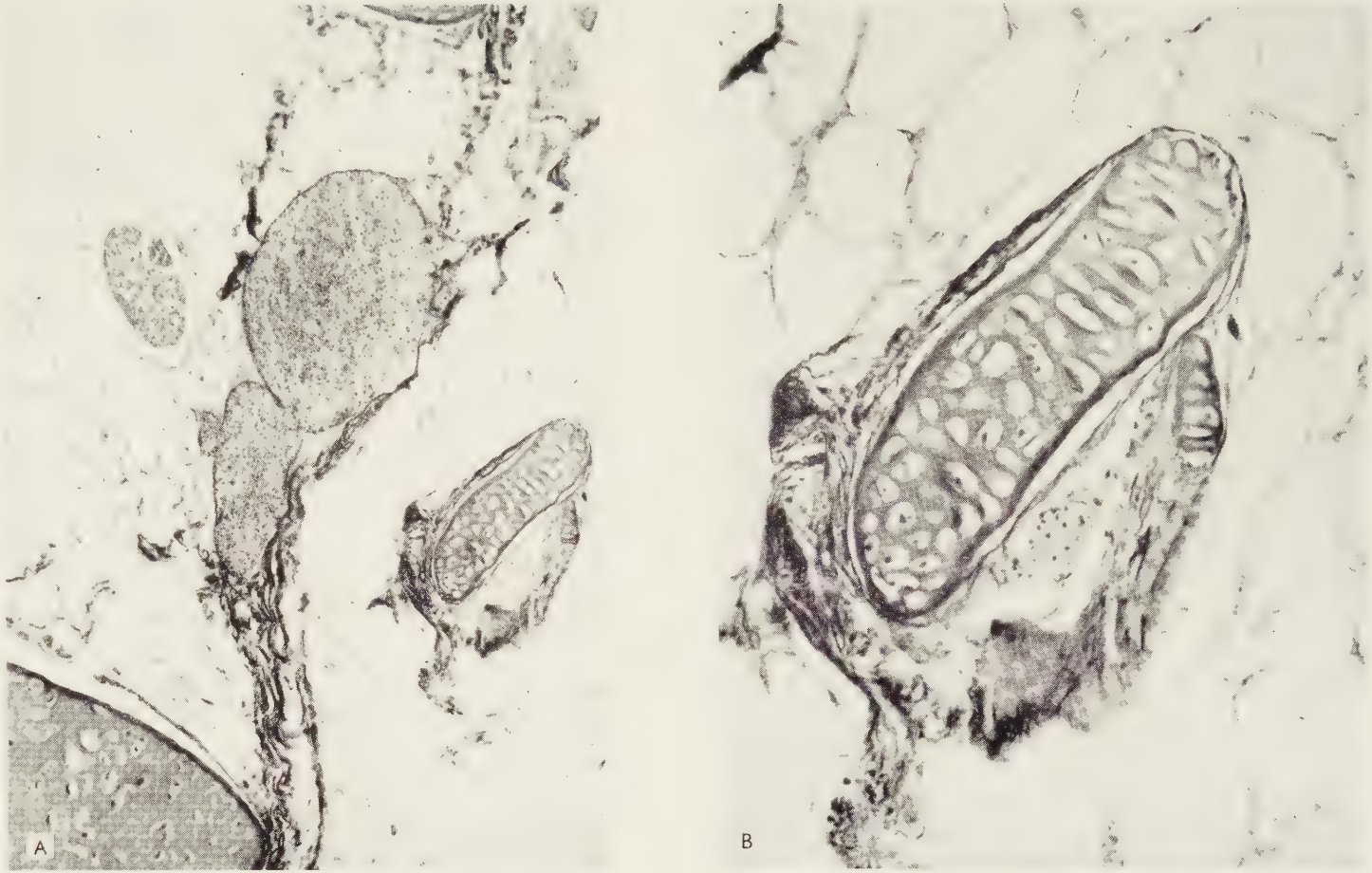
PLATE 2.

A—Transverse section through the head of *Typhlias pearsi* showing on the right the remnants of the eye. These consist mainly of remains of sclerotic cartilage and of some muscular structures, and are imbedded in connective tissue. The regressed ocular structures shown were found 2·6 mm. under the skin surface. Their maximum diameter is ±300 microns. (× 71)

B—Detailed view of the ocular remnants of *Typhlias pearsi*. A small remnant of retinal tissue (?) can be seen in the centre of the vesicle. (× 210)




Sensory degeneration and survival in cave fishes




Sensory degeneration and survival in cave fishes

# THE 'DESIGN' OF FISH AND CEPHALOPOD EYES IN RELATION TO THEIR ENVIRONMENT

BY

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SUMMARY

1. *Density of Medium.* The densities of tissues are usually close to that of water and marine animals derive a great deal of support from the sea. This permits a much greater range in both size and shape in the eyes of marine animals than in those of terrestrial animals. We find enormous eyes in large squid and long stalked eyes such as those of the deep sea fish *Stylophthalmus paradoxus* (Brauer 1906).

2. *The Refractive Index of the Medium.* Because of the high refractive index of water the cornea cannot be used as the major refracting surface forming the retinal image. The refraction in the fish and cephalopod eye is given by a spherical crystalline lens. The fish lens, although it has an aperture of f/0·8, is almost free from both spherical and chromatic aberrations (Pumphrey, personal communication) (Fletcher Murphy & Young, 1954).

3. *The Absorption and Scattering of Light by the Medium.* Pure water does not absorb or scatter visible light very heavily (Le Grand 1939), but natural waters contain dissolved and suspended matter which absorb and scatter light. Even in 'very clear' oceanic waters blue light, which is the light least heavily absorbed, is reduced to about 1/10th for every 60 m increase in depth. The deeper we go in the ocean the more does the penetrating daylight consist of a narrow band of blue light of wavelengths around 475 m$\mu$ (Jerlov, 1947–8 ; Clarke & Werthein, 1956). Because of the strong scattering of light, particularly in coastal waters, it has been generally considered that distant vision would not be very useful to a marine animal and that fishes would be near sighted. This has not, been firmly established by experiment.

4. *Luminescence in the Sea.* At depth and at night the light given by luminescent animals may be more important than the light coming from the sky (Clarke & Werthein). The luminescent light is most often blue or bluish green in colour and often close to that waveband which penetrates oceanic water best. Nicol (1958) has measured both the emission spectra and the energy emitted by a number of luminescent animals. He quotes energy values ranging from $1 \times 10^{-9}$ to about $2 \times 10^{-5}$ $\mu$W/cm$^2$ of a receptor surface at 1 metre from the animal and normal to the emitted light. These fluxes are very small when compared with daylight (the solar constant is 0·135 W/cm$^2$) but they would generally be well above the visual threshold for the dark adapted human eye looking at a small source of light (Pirenne, 1956).

Many animals living in the ocean make daily vertical migrations rising at night and going deeper in the daytime and their eyes will only have

to deal with a relatively narrow range of intensities and will never be exposed to light of high intensities.

The eyes of marine animals not only have to detect the dim penetrating daylight but also patterns of small flashing lights on luminescent creatures.

5. *Pigments in the Eye.* Light will only be useful for vision if it is absorbed by the photosensitive pigments of the retina. There is great interest both in these pigments and those pigments in cornea, lens, and eye media which absorb light before it reaches the retina and so prevent it being used for vision. In fish living close to the surface the lens often contains a pigment absorbing in the blue and near ultra-violet. In deep sea fish such pigments are absent and the lens transmits the blue and near ultra-violet very well (Denton, (1955), (1956); Kennedy & Milkman, (1956); Motais, (1957)). Similarly with squid, those at the surface have lenses which absorb the near ultra-violet (the yellowest of those studied was that of the 'flying' squid *Onychoteuthis banksi*), whilst squid living deeper in the sea have lenses transparent down to about 310 m$\mu$ (Denton, E. J. & Warren, F.J., unpublished observations).

In the past few years it has been shown that the eyes of fishes contain a greater variety of visual pigments than was once thought. (Crescitelli (1959) has recently made an admirable review of our present knowledge of the visual pigments of animals.) It remains in general true that the retinae of fresh water fish have purple coloured pigments whilst the retinae of coastal and deep sea fish have rose and golden coloured pigments respectively. The golden pigments found in deep sea fish are very similar to one another, even although the fish which have been studied come from the most varied families (Denton & Warren, 1957 ; Munz, 1958). Moreover, the fresh-water eel *before* its migration to the deep sea changes its retinal pigment from that typical of a fresh-water fish to one resembling those of the deep-sea fish (Carlisle & Denton, 1959). These facts make it certain that the golden pigments confer some special advantage on deep-sea fish. Some authors (following Barlow 1956 and 1957) have suggested that the main advantage of a shift in maxima of absorption towards the blue end of the spectrum is that the visual pigment will be more stable and that the rate of spontaneous breakdown of visual pigment (of a kind identical to that given by light) will be less. The retina will therefore be less 'noisy' and therefore more sensitive. Wald and Hubbard have argued against this view.

6. *Channelling of Light in the Rods.* In deep-sea fish the rods are usually very long (Brauer, 1908) and the absorption of the incident light by the rods is very high (Denton, 1959). The great length of the rods, although giving great sensitivity may be a disadvantage for acuity unless the light striking the vitreal end of the external segment of a rod is channelled down the rod. If light can pass laterally from one rod to another the eye will be like a camera with a photographic plate of very thick emulsion and the resolution will be very much reduced. This would be particularly true of some deep-sea fish in which the eye is very small and the rods exceptionally long. Experiments are described which demonstrate marked light channelling in the rods of a number of animals, including frog, pike and deep-sea fish. However, even although

observations were not made with light coming to the retina with a lens of aperture as large as that of the fish lens some lateral spreading of light was seen. It does therefore seem likely that in all but the biggest eyes the length of the external segments of the rods must limit acuity much more than does the scattering of light by the layers of retina lying between the rods and the vitreous humour. In some fish this spreading of light is, of course, diminished by the migration of black pigment between the rods and cones.

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# SONIC ORIENTATION OF BATS AND OTHER ANIMALS

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An outline of present knowledge about sonic orientation systems in animals, with special reference to ultrasonic orientations in bats is given. Different types of ultrasonic systems are described and discussed and new experiments concerning the functional role of ear movements in *Rhinolophus ferrum-equinum* Schreb. are reported.

Adaptation is one of the most striking characters of organisms. Structures and functions of the animal organism as a whole and of its organs as parts correspond in an almost perfect manner to the demands of the environment. Therefore it is not surprising to find that sense organs in their specialization are related to the ecology of a given species. The presence or the lack of sense organs, their states of perfection, their mutual functional coordination and cooperation, all this is so closely related to the characters of the specific environment, that by studying the sensory system of a species, we can get a rather detailed picture of the ecological conditions, under which the species is existing, or—if we regard the matter from a standpoint of phylogeny—a picture of the conditions, which called for the evolution of a special and specialized sensory organization.

Such thoughts may help us in considering the problems of sonic orientation systems. What special pattern of environmental demands corresponds to the complicated sonic or ultrasonic systems, which have been recently discovered in bats, whales and birds ? We cannot answer this question here in all details. But as a preliminary answer we may state, that according to our present knowledge, sonic orientation seems to be related to fast, off-the-ground locomotion in complete darkness. This statement certainly simplifies and even violates reality, which is extremely complex, but nevertheless it presents a suitable key to the problems, which we want to discuss here.

The evolution of an acoustical transmitter–receiver system, using reflected sounds to produce a detailed picture of the environment, opened to its owners a unique ecological chance. They were enabled to live in a way and under conditions, where a conventional sensory organization would necessarily fail. They are enabled to fly or to swim with high velocity in complete darkness. If we restrict this to higher vertebrates we can state : nothing but the evolution of a sonic orientation system could enable higher vertebrates, which lack a lateral line system, to move in complete darkness without tactile or olfactory contact with the ground, that is, to swim and to fly in the dark. Up to now sonic orientation systems have only been discovered in animals which fit into the scheme outlined above. A highly efficient system of acoustic orientation (ultrasonic orientation) is known to exist in probably all groups of insectivorous bats (suborder Microchiroptera), where it can dominate over all other senses to such a degree, as to render them rudimentary (Griffin &

Galambos 1941, 1942, Dijkgraaf 1943, 1946, Möhres 1953 a, Griffin & Novick 1955, Möhres & Kulzer 1955, 1957, Novick 1958 a, b, Griffin 1958). Insectivorous bats can be characterized as animals, which are practically " all ear ". There is ultrasonic orientation, combined with very well-developed scotopic vision and olfaction in the genus *Rousettus* of the fruit-bats (suborder Megachiroptera), whilst most other fruit-bats rely upon vision only (Möhres 1953 b, Möhres & Kulzer 1956, Novick 1958 b). Pulses audible to the human ear are the basis of sonic orientation in the oilbird *Steatornis* (Griffin 1953a) and the swiftlets (*Collocallia*) (Novick unpublished, see Griffin 1958), in both cases connected with well-developed scotopic vision. Similar systems may be present in other nocturnal birds, for instance in goatsuckers (Caprimulgidae), though my own experiments with *Caprimulgus europaeus* gave no clear evidence. There is some evidence for sonic orientation in whales, especially in the Odontoceti, though research is still in its beginning and necessarily slow (Lawrence & Schevill 1954, Schevill & Lawrence 1956, Kellog, Kohler & Morris 1953). Suggestions have been made concerning the existence of sonic or ultrasonic orientation systems in different groups of ground-living and climbing mammals (golden hamster, dormice, shrews, rats) (Kahmann & Ostermann 1951, Rosenzweig, Riley & Krech, 1955, Riley & Rosenzweig 1957), but thorough and careful experiments of my own failed to bear them out. Reviewing present knowledge, we can state that sonic orientation is best developed in the Microchiroptera (insectivorous bats), where it reaches an efficiency which can only be compared with the efficiency of vision at its best. At least in some groups of the Microchiroptera sonic orientation reaches a level of perfection, which justifies the term : " image hearing ", corresponding to " image vision ". This highest standard of efficiency is mainly due to the use of ultrasonic waves of high frequency range, the more linear propagation of which, compared with the audible range, favours precision of location and discrimination of most minute details.

The following considerations will mainly be restricted to the orientation of bats. Here our knowledge is most advanced and structural and functional evolution has reached a high level. Moreover, ultrasonic orientation of bats is a field, in which I myself and my collaborators have been able to contribute to progress of knowledge.

There is more variety in the specialization and level of perfection of ultrasonic orientation systems in bats than was originally expected. Griffin and Galambos, in two important papers (Griffin & Galambos 1941, Galambos & Griffin 1942) gave a definite answer to a question, which more than a century ago the famous Italian scientist L. Spallanzani had investigated. The American authors made their experiments with several species of one family of Chiroptera, the family Vespertilionidae, which is the largest family of bats, present on all continents. Griffin and Galambos, after earlier occasional observations of Pierce and Griffin (Pierce & Griffin 1938), discovered, that these animals produce continuously—even when apparently silent for the human ear—volleys of very intense and extremely short ultrasonic pulses, which are used as signals in a sonar system. These signals are different and independent of the well-known high-pitched communication cries of bats.

About the same time and independently the Dutch zoologist Dijkgraaf published similar results with only slight differences in detail (Dijkgraaf 1943). There has been some initial confusion as to the character of these orientation sounds. Dijkgraaf referred to faintly audible sounds, the so-called " ticking sounds—Ticklaute ", while the American authors reported these sounds to be ultrasonic, that means inaudible. But this confusion was soon abolished, as further investigation revealed, that the ultrasonic orientation sounds may have more or less audible components (Griffin 1956). To be just, we should remember that already in 1920 the British physiologist Hartridge had established a hypothesis of an ultrasonic orientation of bats (Hartridge 1920). Unfortunately he failed to support his hypothesis experimentally, so that his ideas were almost forgotten, when a new start was made.

In terms of physics we can generally characterize the orientation sounds of vespertilionid bats as " ultrasonic cracks " or " explosionlike sounds ". The single sound of a volley is usually very short, it lasts only an average of 1 to 3 msec. The pulses may follow each other in the volley with variable repetition rates of up to 300 a second. The frequency spectrum of pulses is generally broad and irregular, though several species possess orientation sounds of narrow frequency range (Möhres & Kulzer 1955, 1957). The sounds have the character of noises. The frequency may be as high as 90 kc/sec and as low as 25 kc/sec in the same pulse. The frequency is high at the beginning of a pulse and decreases towards the end. The amplitude is rather irregular too. There is a sudden initial increase and a slower final decrease, with some irregular maxima in between.

These cracking sounds are produced in the bat's larynx and emitted through the mouth, which may serve as a kind of primitive beaming arrangement. The repetition rate is moderate in free flight, it rises on take-off or landing or when the bat's interest is attracted to an object (Griffin 1953). The intense orientation sounds are reflected by objects in the environment and their echoes are picked up by the ears. The mechanism of ultrasonic orientation consequently can be put out of action both by closing the mouth of the bat and by plugging its ears (Spallanzani 1794, Griffin & Galambos 1941, Dijkgraaf 1943, Möhres 1953). In one case the sender, in the other case the receiver of the sonar system will be switched off. Most bats rely upon ultrasonic orientation to such an extent, that they become quite helpless, if their ultrasonic orientation fails. The other senses are unable to compensate fully for the impairment of the acoustical abilities. In some cases eyes are less rudimentary and can compensate to a certain degree the lack of acoustic information (Möhres & Kulzer 1957).

In the Vespertilionidae the cooperation of both ears is necessary for ultrasonic orientation. Plugging one ear induces turning movements to the side of the unplugged ear (Griffin & Galambos 1941, Möhres 1953).

The physical characters of the signals and the fact that both ears have to cooperate, favours the opinion that the sonar system of the Vespertilionidae acts principally on the basis of time difference estimation. There are many good reasons—more than can be discussed here—for thinking that an echolocating vespertilionid bat mainly estimates the time difference between the

emitted signal and the returning echo as a measure of distance of the reflecting object on the one hand—and the time difference between the arrival of the echo at the two ears as a measure of direction on the other.

In fact, this " time estimation " scheme is a working hypothesis, which has still to be checked against every new result. But it fits the known facts satisfactorily and it provides starting points for further experimental work in this field. I call the type of ultrasonic orientation, in which volleys of explosion-like ultrasonic sounds are used as signals and in which both ears have to cooperate for the evaluation of echos, the " vespertilionid type " of ultrasonic orientation. It seems to exist in a rather uniform way in other families of bats too, for instance in the Molossidae, Emballonuridae, Rhinopomatidae, Phyllostomatidae and others.

At the time when Griffin, Galambos and Dijkgraaf published their discoveries, I myself had also been occupied with problems of bat orientation. Because of the war it was rather late when I realized that the problem I was interested in had already been solved. But soon I became aware that my efforts had only partially been in vain. So far as the vespertilionid bats went, I could confirm the findings of my colleagues. However, I had been occupied mainly with members of another family of bats, the European species of horseshoe bats (Rhinolophidae). Reviewing my findings, I soon recognized that these horseshoe bats represent a different type of ultrasonic orientation mechanism. The most striking external character of these horseshoe bats is that their faces are adorned with the so-called " horseshoe ", a very strange looking and complicated membranous structure, surrounding the nostrils (Fig. 1). The name " horseshoe " fits only partially : it is the most anterior part which resembles a horseshoe. It has the shape of a bowl or a parabolic reflector with the nostrils in the middle. The curvature of the horseshoe can be altered by muscles, which are arranged in a rather complicated pattern in the wall of this structure.

When flying forward the horseshoe bats keep their mouths quite closed and the " horseshoe " is orientated in the forward direction. A similar behaviour can be seen in the resting, but alert, bat. Clinging with its tiny feet to the support, the bat is continuously turning its head into varying directions. The mouth remains closed and the " horseshoe " is always directed towards the objects of interest. The observer cannot but get the impression that this bowl-shaped structure plays an important role in some kind of special sensory perception. My original idea that these bats emit their orientation sounds by the nostrils and that the " horseshoe " serves as a kind of megaphone or focusing device, concentrating the sound into a narrow beam and thus improving the efficiency of ultrasonic orientation, finally proved to be true (Möhres 1953 a). The orientation sounds are produced in the larynx. A tube-like prominence at the top of the larynx fits closely into the palatal opening, thus providing a direct connection between the sound-generating larynx and the sound-emitting nostrils (Fig. 2). But not only in respect to the pathway of sound emission do horseshoe bats differ from vespertilionid bats. Still more significant are the differences between the orientation cries of both groups. These sounds differ in nearly all characters : they are not

explosion-like, but notes of a pure frequency character. They have not an extended spectrum, but consist of almost only one frequency, the value of which is characteristic for the species, though there are slight individual deviations too. The European Greater Horseshoe bat, *Rhinolophus ferrum-equinum* Schreb. produces orientation sounds of about 85 kc/sec. The sounds of the Lesser Horseshoe bat of Europe, *Rhinolophus hipposideros* Bechst. has a frequency of about 110 kc/sec. Compared with the extremely short pulses of the vespertilionid bats, which generally last only some milliseconds, the

Fig. 1.—Head of horseshoe bat. (See text for explanation.)

orientation cries of horseshoe bats are relatively long. For instance, they last on the average 100 msec in the Greater Horseshoe bat. The intervals between the single pulses are consequently rather short. If we regard the physical characters of the orientation cries of the horseshoe bats in detail, we find that these long-lasting pulses have nearly no frequency- or amplitude-modulation. A telecommunication engineer would say that these orientation cries are extremely poorly adapted to the needs of a sonar system, based on

time difference estimation. Above all other features, the sounds are far too long and uniform. At moderate distances the echo must always return, while the signal is still emitted. The difficulties arising from this fact are seriously increased by the fact that horseshoe bats continuously move their heads in varying directions, when orientating. A horseshoe bat can make a quick turn of the head over an angle of nearly 360°, while emitting one single pulse. It is evident that under such circumstances echolocation in a strict sense, an

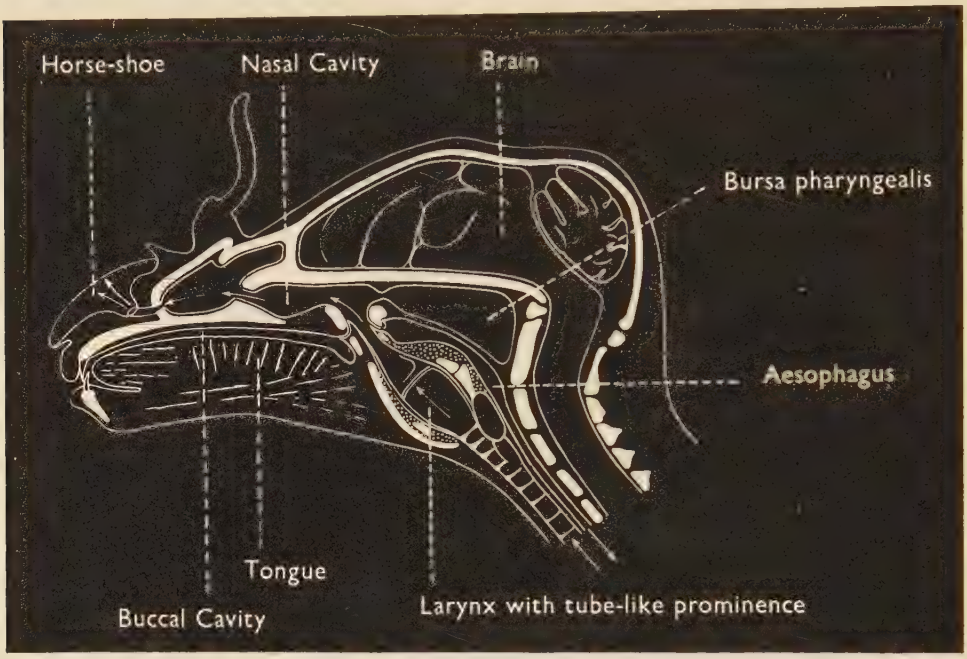


Fig. 2.—Larynx of horseshoe bat with tube-like prominence. (See text for explanation.)

ultrasonic orientation by means of time difference estimation is impossible. On the other hand, observation of the horseshoe bats reveals extremely well developed abilities of object recognition (Möhres 1953 a, Schneider & Möhres 1960).

These considerations lead us to the ears and their role in the mechanism of ultrasonic orientation of horseshoe bats. Here we meet most obvious differences. Ultrasonic orientation in rhinolophid bats is always connected with characteristic movements of the external ears. Whilst the ears of vespertilionid bats are kept almost motionless, in accordance with the time difference estimation scheme, which demands a fixed measuring basis, ultrasonic orientation in the rhinolophid bats is accompanied by very fast and complicated movements of the ears (Möhres 1953 a). These ear movements have recently been analyzed in detail (Schneider & Möhres 1960) and have been found to consist of at least three different components, which are integrated into a complex pattern. The most important of these components is represented by alternating backward and forward movements of the ears.

Of course it is rather improbable that alternatingly moving ears could co-operate in a time difference estimating mechanism. Therefore it is not too surprising to find that they really do not cooperate. Plugging one ear has no essential effect on the efficiency of ultrasonic orientation in horseshoe bats, whilst it proves to be a serious handicap in vespertilionid bats. Plugging both ears has an identical effect in both groups, as can be expected, if a sonar system is really present. One single ear can secure an almost perfect efficiency of orientation in horseshoe bats, whilst in vespertilionid bats this is certainly not so. This and other observations, which cannot be explained here, are, in my opinion, only compatible with the hypothesis, that in the rhinolophid bats the essential feature of ultrasonic orientation is not a time difference estimation, but an intensity difference estimation. In other words, horseshoe bats measure the intensity of their orientation sounds, reflected by the environment, by turning their ears to all parts of the surroundings successively. The movable external ears are consequently regarded as directional sound recorders. This hypothesis, which culminates in regarding the horseshoe bats as representing a special rhinolophid type of ultrasonic orientation, has recently got substantial support by experiments, in which by cutting the motor nerves the ear movements have been partially or totally suppressed. This operation causes a characteristic decrease in exactness of ultrasonic orientation, a deterioriation which after some time is partially balanced, as the animals learn to compensate the lack of ear movements by adequate motion of the head as a whole (Schneider & Möhres 1960).

The rhinolophid type of ultrasonic orientation proves in special tests to be far superior to the vespertilionid type. Appropriate experiments have demonstrated that the Greater Horseshoe bat can recognize a square object of 20 × 20 cm. at a distance of 10 m. (Möhres, unpublished). At shorter distances this species proves to be able to detect nylon strings of only 0·1 mm. diameter. Other rhinolophid species, which produce higher frequencies, can discriminate even still smaller structures, as can be expected according to general laws of physics (Schneider & Möhres 1960, Möhres unpublished). The superiority of horseshoe bats, which according to our present knowledge, surpass all other bats in long and short distance discrimination of objects, and which represent without doubt a summit of evolution of ultrasonic orientation systems, is due to various facts. It is evident that a sonar system with—let us say—" monochromatic " sound must operate more precisely than one which uses " white " noise. On the other hand the megaphone effect of the " horseshoe " provides the possibility of varying concentration of the emitted sounds, according to the distance to be located over. Finally there exists a special focusing mechanism, based on the interference of the two wave fronts, originating from the two nostrils, which contributes to further perfection. Reviewing all known facts, there can be only little doubt that the vespertilionid type and the rhinolophid type represent the ends of two different evolutionary lines, which show only small mutual interdependence.

" Natura non facit saltum "—and a modern biologist is not too fond of strictly separated types. The discovery of the two different highly specialized types of ultrasonic orientation therefore stimulated the search for more

primitive or intermediate stages of evolution. As the approximately one thousand species of living Chiroptera are separated into several well defined families, comparative studies seemed to be promising. We are still in the beginning of such studies (Griffin & Novick 1955, Möhres & Kulzer 1955, 1957, Novick 1958 a, b), but they have already brought new and sometimes very unexpected results.

Space does not permit a full review, and we shall therefore focus our attention on two specially interesting points. Orientation cries of a type intermediate between those of the rhinolophids and the vespertilionids have been found in *Asellia tridens* and other members of the family Hipposideridae (Möhres & Kulzer 1955, Novick 1958 a). The African family Hipposideridae is closely related to the Rhinolophidae. Like these they possess some kind of " horseshoe ", though this structure is different and simpler than in the true horseshoe bats. Their reflector is not parabolic, but cylindrical. The curvature of the hipposiderid " horseshoe " is fixed, it cannot be altered by muscular action as in the rhinolophids. Ear movements are present, but simpler than in the true horseshoe bats. Most astonishing is the character of the orientation cries. In *Asellia* these cries consist of two different well separable parts which generally are both present, though one or the other may be lacking under certain conditions. The initial part of such a combination sound resembles the orientation sounds of the rhinolophid type, it is a pure tone of fixed frequency. In *Asellia* this first part has a frequency of 120 kc/sec. The end part represents an explosion-like sound of lower frequencies, comparable with the orientation sounds of the vespertilionid type. This part has a rather extended frequency-spectrum, with an intensity maximum between 45 and 60 kc/sec. Experimental analysis of this aberrant type of ultrasonic orientation is not yet complete, but there is little doubt that the " rhinolophid " part of these combination sounds facilitates a very exact recognition of objects at short distance, whilst the following " vespertilionid " part serves for more inexact echolocation at a greater distance. If for instance *Asellia* is interested in more remote objects, only the second parts of the orientation sounds, the explosion-like sounds, will be produced in quick repetition. For other hipposiderid bats Novick has given similar oscillogramms of orientation sounds, but he was unable to perform orientation experiments (Novick 1958 a).

Perhaps still more interesting and fascinating are the results obtained from a study of ultrasonic orientation in certain fruit bats (Megachiroptera). Most fruit bats or flying foxes lack ultrasonic orientation altogether ; they depend on vision only (Möhres 1953 b, Möhres & Kulzer 1956, Novick 1958 b). All fruit bats possess very big and efficient eyes, specially adapted to dim vision. As they feed on fruit, olfaction is well developed too, quite in contrast to the Microchiroptera. Only one cave dwelling genus of fruit bats has been found to possess ultrasonic orientation besides well-developed vision and olfaction. This is the genus *Rousettus*. The orientation sounds of *Rousettus* belong to the vespertilionid type and the method of the sonar system seems to be based on time difference estimation. Under these circumstances there was a strong temptation to regard *Rousettus* as a model of an earlier stage of

evolution of the vespertilionid type, a stage in which an ultrasonic orientation system had already been evolved, but the other leading senses were still in full action and by no means rudimentary. There seemed to be connections with the evolution of the rhinolophid type too. These fruit bats of the genus *Rousettus* with their well-balanced sensory organization offered nearly all material for the construction of an admirable evolutionary scheme. But detailed studies finally proved all such phylogenetic speculations to be without a real basis. The pity is that these *Rousettus* produce their orientation sounds in a manner quite different from insectivorous bats. While these generate their orientation sounds in the larynx, *Rousettus* produces rather similar sounds by quick oscillations of the tongue (Kulzer 1956). In a very careful and profound study Kulzer (1960) has clarified the mechanism of sound production in *Rousettus*. Compression and sudden dilatation of two air cushions in two small areas on both sides of the *frenulum linguae* produce characteristic twin-groups of explosion-like sounds, which are emitted at a rather high repetition rate. This is the first time that we have obtained full information about a mechanism for the production of ultrasonic orientation sounds, which provides valuable progress of knowledge in this field on the one hand and on the other a tomb for phylogenetic speculation which at first sight appears rather reasonable. Ultrasonic orientation in *Rousettus* must have been independently evolved.

Summarizing our present knowledge we may say that ultrasonic orientation of bats and fruit bats provides fascinating examples of sensory mechanisms developed in response to most special environmental demands and evolved to an admirable level of perfection. But the origin and the ways of the evolutionary lines remain hidden in the darkness of the past.

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# THE SENSITIVITY LIMITS OF PHOTORECEPTORS

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It is important that all the information which can be derived from experiments on the spectral and absolute threshold sensitivity of animals should be extracted and presented. This can only be done if narrow bands of wavelengths are used and the light flux is measured in energy units. The apparatus, methods and calibrations which can be used are discussed from the point of view of obtaining the maximum information and presenting it so that it can be compared with the results of other workers. Measurements made on five species—man, the cat, the owl, *Xenopus* and the flatworm *Dendrocoelum*—are discussed and compared, with special reference to the differences between the eyes of these animals.

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## INTRODUCTION

A great deal of experimental work has been done on the visual sensitivity of animals. The problems investigated include spectral sensitivity, absolute light sensitivity, and colour discrimination. These experiments are usually difficult and time-consuming, and it is therefore important that all the information available from the experimental results should be extracted and correctly interpreted.

Comparison between the experiments of different authors is only possible if they are published with full details of the apparatus, animals, and measurements, and if these details are given in such a form that another worker could do the same experiments from the description given. There is a very strong

case for the standardization of apparatus and measurements. The use of arbitrary units or imperfectly specified sources means that much of the information which could be derived from the experiments is never made available.

It is not always easy to control conditions and calibrate apparatus so that measurements can be made in a uniform way and expressed in a standard form. Nevertheless these difficulties can usually be overcome, and the value of the results is thereby enormously increased.

The first part of this communication will be concerned with the apparatus which can be used for the experiments, the precautions which should be taken, the measurements and calibrations which are needed, and the presentation of results. These comments apply to all visual experiments in which quantitative results are to be obtained. The specific problem considered is that of the absolute visual threshold, and this involves, as will be seen, the measurement of spectral sensitivity. The special difficulties involved in the detection and assessment of colour vision in animals will not be considered.

In the second part measurements of the absolute sensitivity of a few animals (including man) will be discussed. These experiments exemplify the ideas of the previous discussion, and the results make possible a direct comparison between animals drawn from widely different classes.

## PROBLEMS OF VISUAL SENSITIVITY MEASUREMENT

### *The visual stimulus*

There are considerable differences between the spectral sensitivities of different species of animal. The ordinary photometric units are defined in terms of the photopic (cone) spectral sensitivity of man. For this reason such units are unsuitable for describing the visual performance of other animals unless it has been shown that the animals have spectral sensitivity curves similar to the human photopic curve. They are equally unsuitable for describing measurements of human scotopic (rod) sensitivity without complete specification of the light used, since the sensitivity curve for rod vision is quite different from that for cone vision.

The use of white light in sensitivity measurements is also ruled out unless the spectral sensitivity is accurately known. White lights of equal photopic luminance may have quite different spectral composition, and if so they will have entirely different effective luminance for, say, an animal which is more sensitive than man to light of short wavelength. The well-known Purkinje shift shows how misleading the use of white light, specified only in photopic luminosity units, can be. The human scotopic sensitivity curve is accurately known, and white light can be used for threshold measurements ; but the " colour temperature ", which describes the spectral composition of white light, must be taken into account, and the results expressed either in special scotopic photometric units, or, preferably, in terms of scotopically equivalent monochromatic light.

The only satisfactory method of measuring spectral or absolute sensitivities is to work with isolated bands of the spectrum and express all results in terms of energy units, such as ergs or, more fundamentally, light quanta. Since

spectral sensitivity curves do not, in general, show large irregularities or changes for variations in wavelength of a few mμ, very narrow wavebands are not necessary. Narrow band colour filters such as Ilford " spectrum " filters, or interference filters are usually satisfactory for experimental purposes, but if they are used allowances must be made in estimating the spectral sensitivity, and the final results must be expressed in terms of monochromatic light (Denton & Pirenne, 1954 a).

If a large retinal area is stimulated, it should be measured, so that the results can be expressed in terms of retinal illumination. If the area is small—for example a distant effectively point source viewed by an emmetropic eye—then the total energy entering the eye is required. The most useful experiments are those using either a very short flash of known duration, or a long exposure time of several seconds. The results can then be expressed either as total energy in the former case, or energy per second in the latter. The units may then be summarized as in Table 1.

TABLE 1

| | Brief flash | Long exposure |
|---|---|---|
| Small field | erg (λ) | erg (λ)/sec |
| Large field | erg (λ)/cm² (retina) | erg (λ)/cm² (retina) . sec |

(Erg may be replaced by quanta)

This is not necessarily the most convenient way of expressing the results from a practical point of view. It may, for example be important to know whether an animal can detect a specified light, and to answer this question from data expressed as in Table 1 involves a knowledge of the pupil size and perhaps the power of the eye. But for comparison of the physiological performances of different animals, the units of Table 1 are the most appropriate.

### *A simple apparatus for visual stimulation*

Fig. 1 shows the apparatus used by Pirenne and his collaborators for many of their experiments. A source L consisting of a tungsten-filament bulb is mounted in a light-tight box behind a diaphragm. A colour filter F is mounted in front of the diaphragm, and neutral wedges W control the intensity.

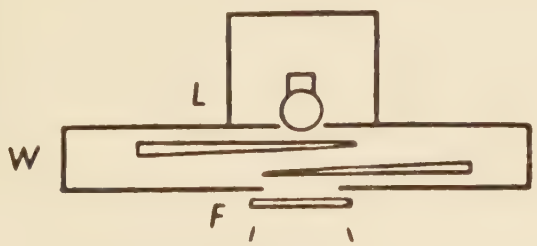



Fig. 1.—Apparatus for producing variable light stimuli which can be expressed in terms of the energy in narrow spectral bands.

L—calibrated tungsten-filament bulb.
W—neutral wedges.
F—colour filter.

This basic apparatus can be used in various ways. Placed at a considerable distance from the experimental animal, it can be regarded as an effectively point source. If it is placed in front of a lens and focused on the pupil of the eye of the animal, it provides a reasonably uniform large field seen in Maxwellian view. A shutter mounted in front of the source makes it possible to give flashes of controlled duration. Thus the apparatus may be used to give stimuli of the four types listed in Table 1.

This simple apparatus is extremely versatile, and, when calibrated, can be used to measure spectral and absolute sensitivities under a wide variety of conditions. It has been employed, without major modification, for experiments on man, the cat, *Xenopus*, and the flatworm *Dendrocoelum*. In the following sections the constituents of a visual stimulator will be discussed with special reference to this apparatus.

### *The light source*

A tungsten-filament bulb provides a light-source which is simple, stable, and durable. It should be " aged " before use, and later underrun at an accurately controlled temperature, and occasionally compared with a standard source, to ensure stability. For practical purposes the relative spectral energy distribution of the bulb is that of a Plankian perfect radiator, or " black body " ; if, therefore, the colour temperature and luminance are known, the energy output in any narrow spectral band can be calculated. There are minor inaccuracies near the ends of the visible spectrum, but the approximation is quite adequate unless ultra-violet or infra-red sensitivity is required, when special calibrations are needed.

The main drawback of the tungsten-filament bulb is that it has a low output for very short wavelengths. The ultra-violet output is also reduced if the bulb is made of glass, which filters out much of the short wavelength radiation. If it is necessary to investigate ultra-violet sensitivity, some other source must be used. Xenon or mercury discharge tubes may be used, but need careful calibration and frequent checking.

The use of photo-electric cells or thermopiles for calibration involves considerable difficulties, and their limitations must be clearly understood. The photoelectric cell is usually designed to have a response curve similar to the photopic sensitivity of the human eye. Unless it has been accurately calibrated for spectral response, it is useless for comparing the intensities of lights of different spectral composition for purposes of animal experimentation. The thermopile responds to the total energy striking it, regardless of wavelength. The response to a white light is largely determined by the amount of infra-red radiation. In any case, the apparatus is difficult to use. Usually it is much more satisfactory to use a calibrated source in the way outlined above.

### *The neutral wedges*

The most satisfactory way of controlling intensity is by means of neutral wedges. These must be calibrated for light transmission along their length, and it is also necessary to check their spectral absorption, since such wedges are not strictly neutral, especially when high densities are used.

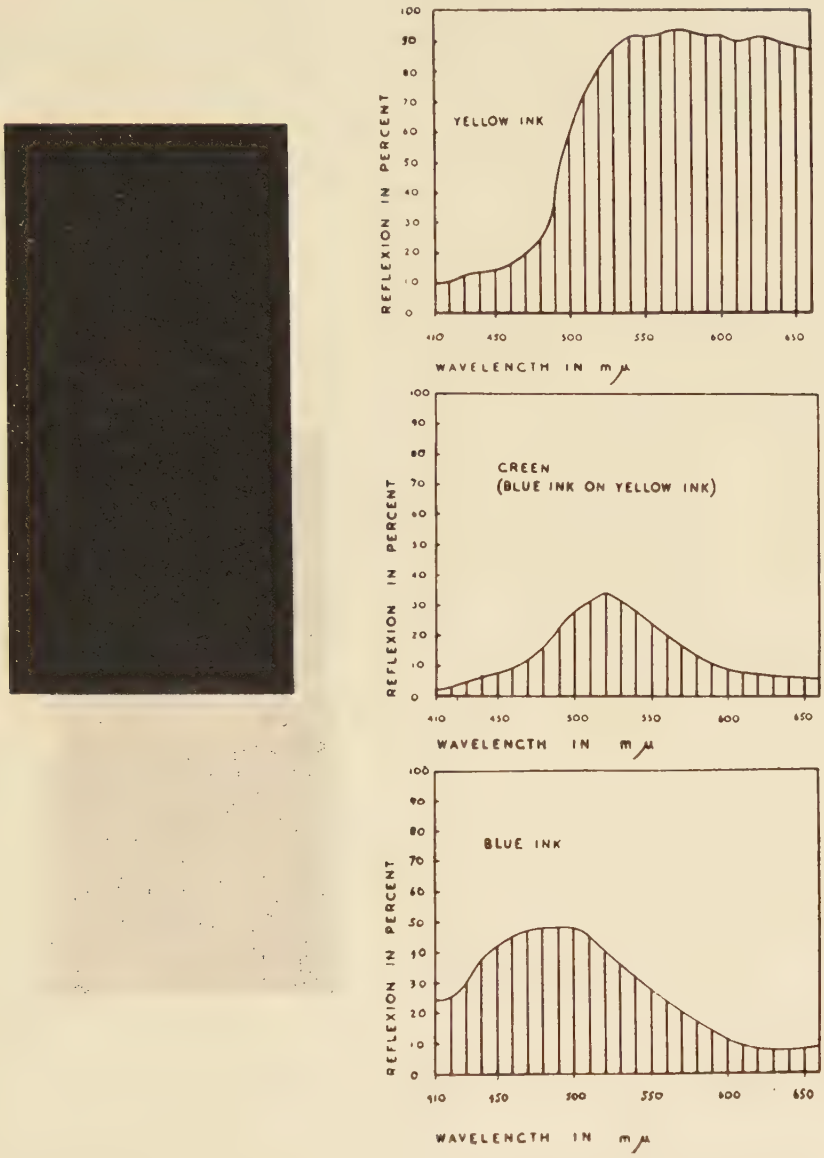



Fig. 2.—Spectral reflexion curves of various inks. The reflected ligh rarely falls below 5 per cent for any wavelength, whatever the colour of the surface (Pirenne, 1948).

The use of a rheostat to vary intensity is unsatisfactory since it also changes the colour temperature, and this makes the calculation of energies much more difficult. A given change in voltage produces quite different changes in the outputs of red and green lights. Thus, if the intensity is varied in this way, it is necessary to calibrate the bulb for every voltage used.

*Colour filters and monochromators*

A monochromator is a cumbersome device, and is expensive and difficult to construct and use. If really accurately controlled narrow bands of wave-

lengths are required, then it is necessary ; it is used, for example, in experiments on human colour vision. But it is difficult to eliminate stray light, and to get adequate light-intensities. It should not be considered unless colour filters would certainly not be sufficiently accurate.

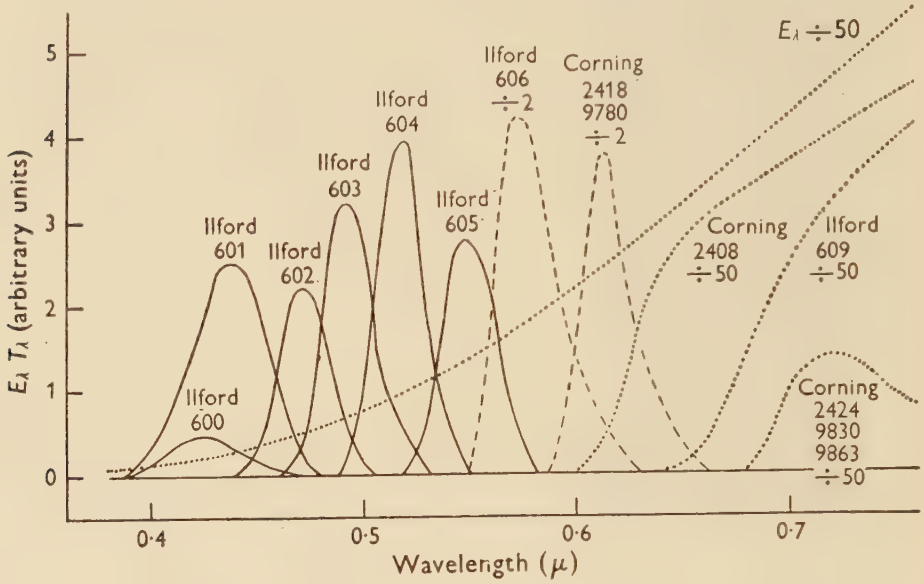



Fig. 3.—Spectral transmission curves of a series of colour filters (Denton & Pirenne, 1954 a).

Interference filters may have comparatively narrow transmission bands, and if so they can be regarded as transmitting effectively monochromatic light, which simplifies the calculations. It should not be assumed, however, that the only light transmitted is in the main waveband. There may well be side bands, and transmission of even a very little light of a wavelength more effective than the principal one can completely vitiate experimental results.

Interference filters usually transmit relatively more light than pigment filters at a considerable distance from the main waveband—that is, the spectral distribution has long " tails ". This may make it necessary to use them in conjunction with another filter, especially if the main waveband is one to which the animal is relatively insensitive. The narrow band of wavelengths transmitted also has the disadvantage that it is difficult to get adequate intensities.

Pigment colour filters of one of the special " spectrum " or " monochromat " series are quite satisfactory if they are properly calibrated. The maker's calibration is not, as a rule, particularly accurate, and the spectral transmission should be measured for each individual filter. Side bands may occur, and most filters transmit the infra-red. The comparatively wide bands transmitted do not invalidate the experiments, though they do make calculations more complicated.

Light reflected from pigments is not, as a rule, satisfactory. Coloured objects reflect considerable amounts of light throughout the spectrum ; even

black paper may reflect as much as 10 per cent of the light incident upon it. Now in human scotopic vision light of wavelength 600 mμ is only 1/20 as efficient as blue-green light and at 700 mμ the efficiency has fallen to 1/10 000. Thus a deep red paper illuminated by white light may well reflect a flux of green light which is more effective in scotopic vision than the red light which it reflects. Fig. 2 shows the spectral reflexion curves of paper coloured with various inks. Fig. 3 shows, by contrast, the transmission curves of a series of colour filters.

### *The shutter*

The ordinary photographic shutter is not a particularly satisfactory device. In my experience they are fragile, unreliable, and apt to develop light leakages. For long exposures they are probably the simplest solution, but for short flashes it is hard to feel much confidence in them.

Pendulum shutters and rotating disk shutters are less convenient, but far more reliable. If accurately controlled brief flashes are required, it is much more satisfactory to use one of these types.

Various types of electromagnetic shutter have been devised for special purposes. They are too complicated for general use, and should only be considered for special applications, such as successions of flashes.

### *Experimental animals*

Before the light sensitivity of an organism can be measured it is necessary that it should show a recognizable response to a light stimulus. The responses which can be used are of three types :—

(1) A natural response. This includes the behavioural responses of many lower organisms—tropisms, increases in activity, and so on—and such responses as pupil contraction or colour change.

(2) A conditioned response. Many animals can be trained to respond to light stimuli.

(3) Electrophysiological responses. These include recordings from the optic pathway with gross or micro-electrodes, and the electroretinogram.

It is not certain in any of these cases that the threshold of the response is the same as the threshold for " seeing ", defined in some other way.

In the case of natural responses, there may be responses other than the one chosen for experiment which have a lower threshold ; for example an animal may show increased random activity at a lower luminance level than that at which it exhibits a directional response. On the other hand, a light response does not necessarily imply that the visual system has been stimulated—responses such as pigmentation changes may be mediated by light sensitive organs in the skin.

Animals trained to respond to light may not do so unless it reaches a level well above that which they can detect, just as an inattentive human subject may not reach the physiological limits of his visual performance. On the other hand, the example of " subliminal advertising " shows that it may

be possible to produce a response to visual stimulation in man without *conscious* visual sensation.

Electrophysiological responses have the same limitations. A response at, say, the retina may not be propagated to higher levels. On the other hand it is not, as a rule, possible to say that none of the nerve cells has responded to the stimulus. Anaesthetics and surgical procedures introduce further uncertainties into the interpretation of an electrophysiological response in terms of " seeing ".

Yet a further difficulty arises in the case of animals with colour vision. The animal may respond to lights which stimulate certain colour mechanisms but not to others. This would, of course, invalidate estimates of the spectral sensitivity curve. The point is often unimportant, however, since in animals with mixed retinae (rods and cones) the *threshold* is usually determined by the rods for most wavelengths.

All these experiments therefore measure the threshold for a response, and to describe the measured value as the threshold of vision involves an additional assumption. If workers measuring the thresholds for different responses obtain different results, this is not in the least surprising.

### *General observations on visual sensitivity*

The spectral sensitivity of man is well known. Maximum sensitivity is at about 507 m$\mu$ for rod vision and 555 m$\mu$ for cone vision, and radiations of wavelength less than 400 m$\mu$ or more than 700 m$\mu$ have very low luminosity. If intensities are sufficiently high, it is possible to detect wavelengths of 315 m$\mu$ in the ultra-violet and 1000 m$\mu$ in the infra-red. The limits of the visible spectrum are not sharply defined, but the range 400–700 m$\mu$ includes most of the visually effective light.

The visual ineffectiveness of the ultra-violet is largely due to absorption by the eye media, and in particular by the lens. Wald has shown that aphakic subjects are much more sensitive to short wavelengths than normal subjects. It must always be taken into consideration that animals, especially those which have not a lens of the type found in most vertebrates, may be relatively more sensitive than man to short wavelengths. This has been demonstrated for *Dendrocoelum*, and von Frisch has shown that bees have a colour vision mechanism especially sensitive to this part of the spectrum. Ultra-violet sensitivity would be of little advantage to man or to animals with similar eyes, since chromatic aberration would make image formation extremely bad.

Infra-red radiation has quanta of relatively low energy, and its visual ineffectiveness may be largely due to the inability of such quanta to act on the molecules of visual pigments. Since the body itself acts as a source of infra-red radiation (mainly of wavelength greater than 3000 m$\mu$, but of appreciable amounts down to 1000 m$\mu$), sensitivity to wavelengths in this range would be of no biological value—radiation reaching the retina from external objects would be swamped by radiation from the eye itself and its surrounding tissues. It was at one time suggested that the owl could see small animals in total darkness by detecting the infra-red radiation from their bodies ; for the reasons adduced this appears impossible. No animal has been shown to have much

greater visual sensitivity than man to long wavelengths. The pit vipers, however—cold blooded animals—have a special organ which can detect radiation from animals with considerably higher body temperatures. (Noble & Schmidt, 1937.)

## THE ABSOLUTE VISUAL SENSITIVITY OF CERTAIN ANIMALS

### *Man*

Since visual sensitivity has been studied in more detail in man than in other animals, it is convenient to consider human scotopic sensitivity first, and discuss the performance of other animals relative to it.

As is well known, the human scotopic spectral sensitivity curve has a maximum at about 507 m$\mu$. The curve is fairly accurately known, and so experiments done with lights of any spectral composition can be interpreted in terms of radiation of this wavelength.

When a small field is exposed in a brief flash, the human eye, fixating at 20° from the test field, can detect a light flash of $2\text{–}6 \times 10^{-10}$ erg (507 m$\mu$). This corresponds to about 50–150 quanta striking the cornea, or about 5–15 quanta absorbed by the retina (Hecht, Shlaer & Pirenne, 1942).

The corresponding figure for a small source and long exposures (with free eye movement) is about 90–150 quanta per sec. at the cornea (Marriott, Morris & Pirenne, 1959 a).

For a large field (47°) exposed in brief flashes, the threshold is about 3000 quanta (507 m$\mu$)/cm$^2$ (retina), or about $1{\cdot}2 \times 10^{-8}$ erg (507 m$\mu$)/cm$^2$ (retina) (Hallett, unpublished result).

For a large field (47°) continuously exposed, the threshold is about $9 \times 10^{-8}$ erg (507 m$\mu$)/sec $\times$ cm$^2$ (retina), or about 22000 quanta (507 m$\mu$)/sec $\times$ cm$^2$ (retina) (Pirenne, Marriott & O'Doherty, 1957).

Fig. 4 a shows the receptors of the human peripheral retina (Schultze, 1866), and Fig. 5 is a diagram of the human eye (Schäfer & Thane, 1894).

### *The cat*

The cat is primarily a nocturnal animal and, compared with man, its eye shows various features which are adapted to night vision. But the adaptation is not extreme, and the differences from the human eye are much smaller than in the case of, for example, the owl.

The retina contains few cones, and the fovea is virtually absent. Part of the sclera is covered by a reflecting tapetum which increases the effective absorption by the retina by a factor of about 1·4. The maximum pupil area is greater than in the human eye. The eye is roughly spherical, and the rods are similar to the human rods in shape, but somewhat smaller.

Fig. 4 b shows the receptors of the cat's retina (Schultze, 1866). Fig. 6 shows a section of a frozen cat's eye (Davson, 1953).

Gunter (1951, 1952) measured the spectral sensitivity and absolute threshold of the cat. He trained cats to open a door to obtain food when the door was illuminated. The spectral sensitivity was closely similar to the human scotopic curve. The threshold (for a large field and long exposure) was $0{\cdot}20\text{–}0{\cdot}39 \times 10^{-6}$ cd/m$^2$ ; mean $0{\cdot}32 \times 10^{-6}$ cd/m$^2$ ; two human subjects

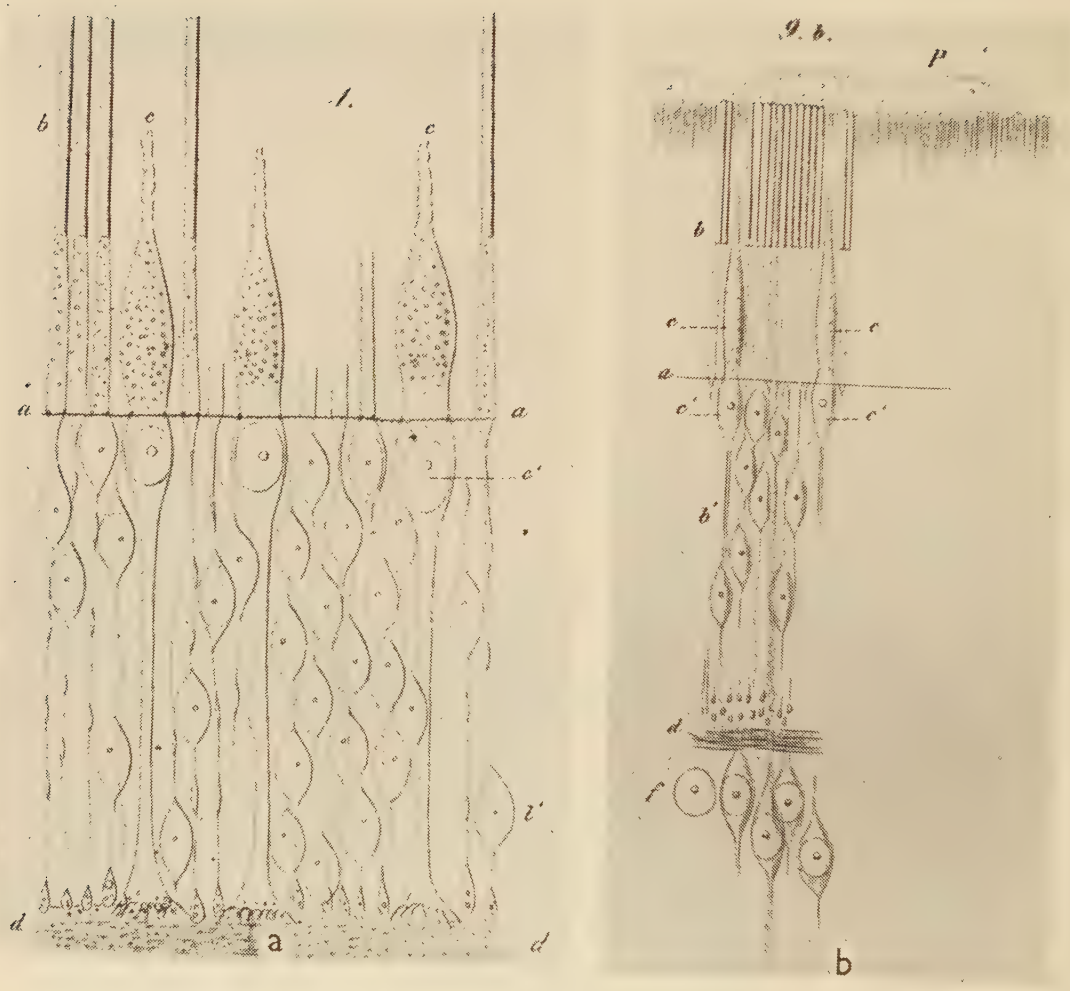
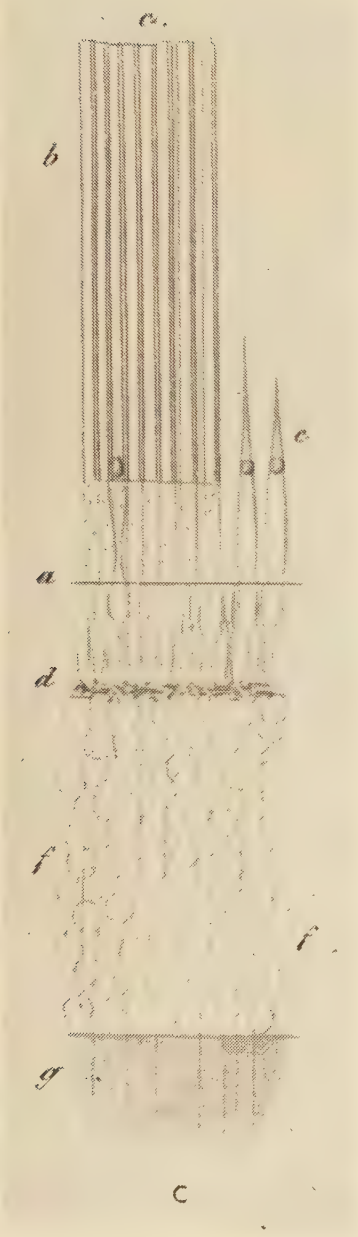



Fig. 4, a, b.—Rods and cones in various retinae (Schultze, 1866). a. The human retina, in the periphery. b. The cat. [*Continued next page*]



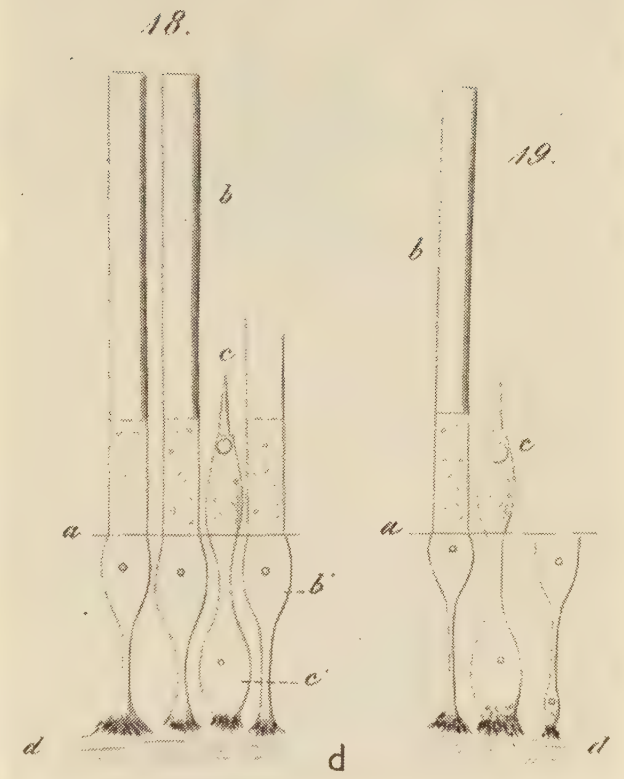




Fig. 4, c, d.—Rods and cones in various retinae. c. The owl. The very long rods are adapted for nocturnal vision. d. The frog. The receptors of *Xenopus laevis* are similar, but smaller.

measured with the same apparatus gave a mean threshold $1{\cdot}74 \times 10^{-6}$ cd/m$^2$, or about six times that of the cat. Bridgman & Smith (1942) found similar results.

[Candelas per square metre, the photopic units of luminance, are not appropriate here, as has been explained. The figures for cat and man, however, may be validly compared, since the same source was used and the scotopic spectral sensitivities are similar.]

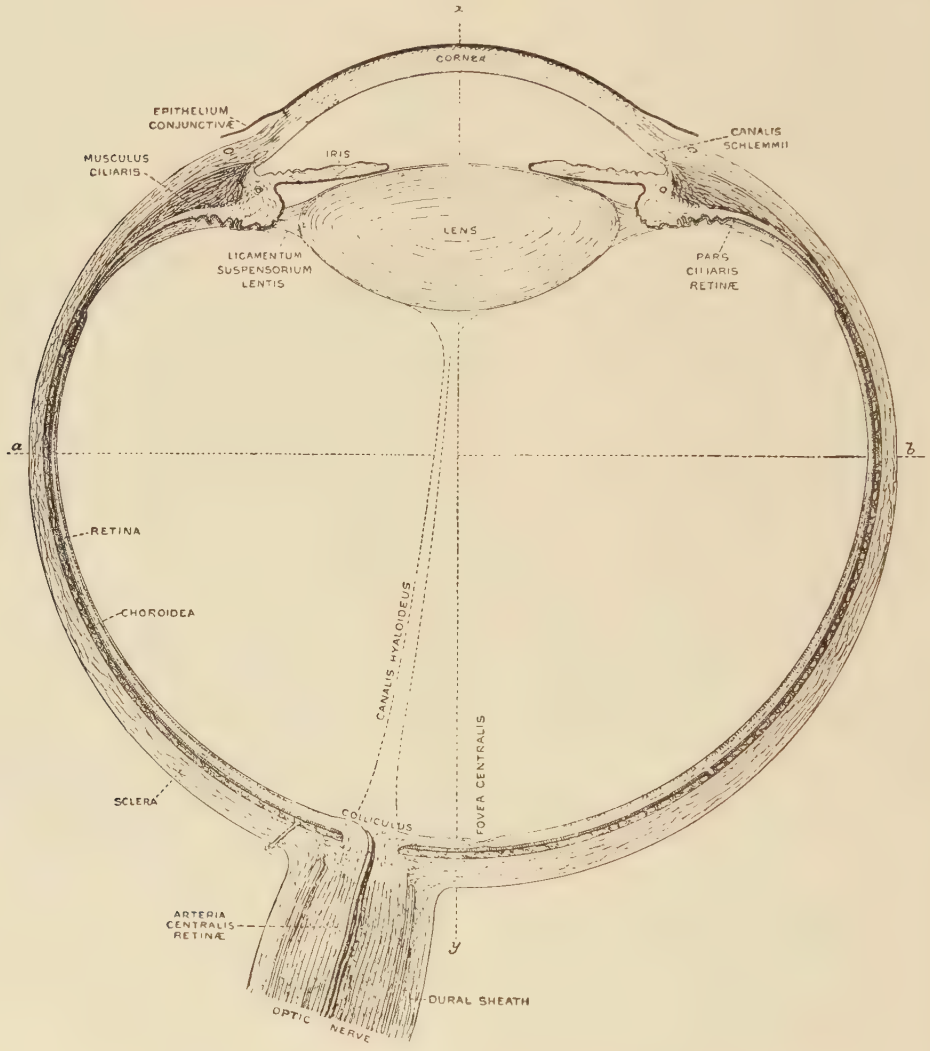



Fig. 5.—The human eye (Schäfer & Thane, 1894).

The difference between the thresholds of cat and man is approximately accounted for by the effects of the larger pupil, greater power, and tapetum of the cat's eye (Weale, 1953). Thus the effective retinal illumination at threshold is roughly the same for man and cat. The comparison is not accurate, since there are large individual variations in both species.

Marriott, Morris & Pirenne (1959 b) calculated that Gunter's value corresponded to a retinal illumination of $2{\cdot}4 \times 10^{-7}$ erg (507 m$\mu$)/sec. cm$^2$ (retina). This calculation is only a rough approximation, since the characteristics of the eyes of the cats used by Gunter are not accurately known. From electrophysiological preparations Marriott *et al.* obtained responses, in one case, to an illumination of $7{\cdot}4 \times 10^{-7}$ erg (507 m$\mu$)/sec. cm$^2$ (retina). The recordings were obtained with Wollaston wire micro-electrodes in the lateral geniculate body, but were not from single nerve cells.

Fig. 6.—Section of a frozen cat's eye (Davson, 1953).

Thus the threshold recorded electrophysiologically was only three times that obtained from the intact cat. Professor Whitteridge, however, has pointed out that the anaesthetic used, Nembutal, can in some circumstances impair retinal localization. It is therefore possible that the cells from which the recording was made were responding to a larger retinal area than they would in the intact animal, and the remarkably close agreement with Gunter's result may have been a coincidence due to a combination of disturbing factors. Attempts to measure the retinal area to which single nerve cells respond have given very variable results. Barlow, Fitzhugh & Kuffler (1957) obtained rather higher thresholds using electrophysiological recording from retinal ganglion cells.

*The owl*

The owl is a nocturnal bird with an eye very strongly adapted for nocturnal vision. The eye is of enormous size relative to the size of the head, and occupies a large part of the skull (Fig. 7). It is of a bulbous shape, not unlike the tubular eye of some deep sea fishes. It is almost completely fixed in the head, facing forward, and is aligned by head movements. The pupil is very large, the retina contains predominantly rods, and these are very long structures, so that presumably they absorb a high proportion of the light incident upon them (Fig. 4 c). There is a tapetum.

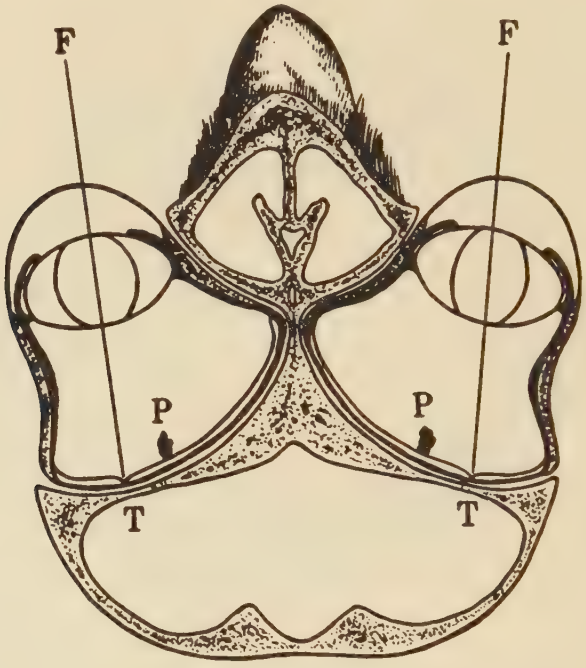



Fig. 7.—The head and eyes of the owl. The eyes are similar in shape to the tubular eyes of certain abyssal fish.

Hecht & Pirenne (1940) measured the spectral sensitivity of the long-eared owl *Asio wilsonianus*, using the pupil contraction. The spectral sensitivity was found to be similar to the human scotopic curve.

The supposed sensitivity to infra-red radiation was investigated. Matthews & Matthews (1939) showed that wavelengths near 9000 m$\mu$ produced no detectable effect on the electroretinogram, and that, in any case, they were absorbed in the optic media before reaching the retina. Hecht & Pirenne showed that if wavelengths less than 750 m$\mu$ were excluded, light from the stimulator lamp produced no pupil contraction even at energy intensities $5 \times 10^6$ times above the threshold energy of green light for this response.

The threshold for the pupil contraction in terms of external illumination was about 400 times the human absolute threshold. In the human eye, pupil

contraction occurs at an illumination of about 1000 times the absolute threshold (Reeves, 1918).

It is well known that owls are extremely sensitive to dim lights; Dice (1945), for example estimated that the long-eared owl could detect dead mice at a light intensity about 10–100 times below that at which a man could detect them. It must be emphasized that this does not imply that the owl can respond to a lower *retinal* stimulus than man. The large pupil and high power of the eye produce a relatively higher retinal illumination than in man for a given external luminance, and the retina is probably optically denser than that of man. The human eye can detect a light flash in which only a few quanta act on the retina (Hecht, Schlaer & Pirenne, 1942), and so the threshold of the owl certainly cannot correspond to a much smaller amount of light actually acting on the retina.

*Xenopus laevis*

Denton & Pirenne (1954 b) measured the spectral and absolute sensitivity of the toad *Xenopus laevis*. *Xenopus* has eyes rather similar to those of the frog, but relatively smaller. They are placed on the top of the head. The retina contains two types of rod, red and green, and small cones (*cf.* Fig. 4 d).

Two responses were used for the experiments, melanophore expansion, which causes blackening of the skin, and "escaping from light" into a darkened part of the box. The maximum sensitivity was found to be at about 560 m$\mu$. The absolute threshold for the melanophore response was 600 000 quanta (560 m$\mu$)/sec. cm$^2$ (retina), that is about 20 times the corresponding figure for man.

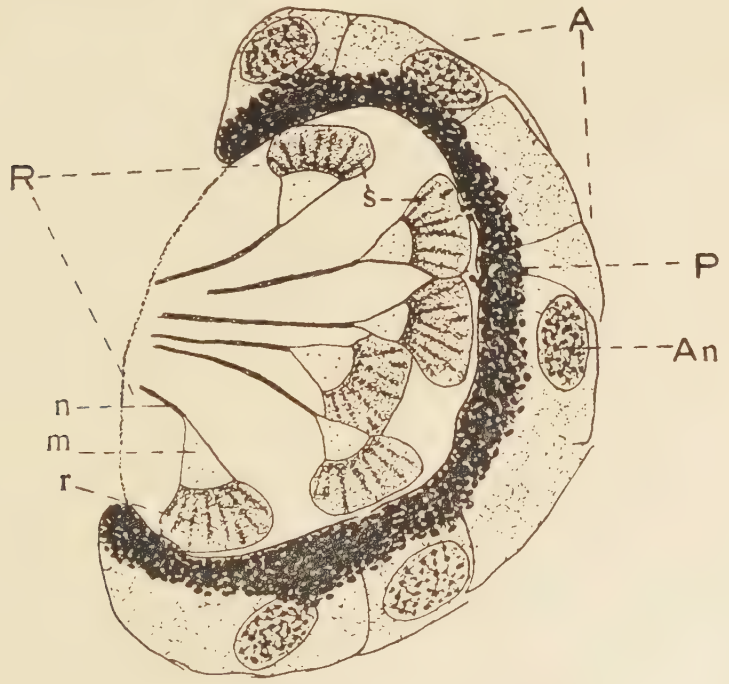



Fig. 8.—The planarian eye. (Taliaferro, 1920)

### *Dendrocoelum lacteum*

*Dendrocoelum lacteum* is an aquatic flatworm about 0·5–1 cm. long, creamy white in colour, with two black eyespots about 0·08 mm. in diameter at the anterior end. It moves away from light, and this response is mediated by the eyespots. Fig. 8 shows the eye of *Dendrocoelum*, a simple pocket, without lens or other focusing arrangements, containing a few receptor cells.

The spectral sensitivity curve in the range 420—700 mμ is rather similar to the human scotopic curve, but the animal is relatively much more sensitive to short wavelengths (Viaud, 1950 ; Marriott, 1958). The curve, in fact, resembles that of the aphakic human eye (Wald, 1945). This is what would be expected if the animal had a retinal pigment similar to human rhodopsin, since there can be very little absorption in the preretinal structures. The mean absolute threshold corresponded to about 39 000 quanta (520 mμ)/sec. per eye. This compares with the human threshold of about 120 quanta/sec. for a small source continuously exposed (Marriott, Morris & Pirenne, 1959 a) and the retinal area illuminated is probably similar. The most sensitive animals responded at 1/10 of this intensity, and if the size of the opening of the eyespot is taken into account the threshold of these animals is only about 20 times that of man in terms of quanta striking the eye.

## CONCLUSION

The visual sensitivity of five animals, from four different orders, has been discussed. The eyes, and the visual sensitivities, differ enormously, ranging from the highly specialized eye of the owl with its adaption for collecting light in nocturnal conditions to the eye of *Dendrocoelum*, which is little more than a pocket of light-sensitive cells.

Yet in spite of these differences, perhaps the most remarkable feature of the results is the small range in visual sensitivity in terms of retinal illumination. The retina of the owl is probably a little more sensitive than that of man ; the eye of *Dendrocoelum* is only about 20 times less sensitive.

It is well known that the human retina can respond when only a few molecules of rhodopsin are acted on by light. Clearly no visual system can be much more efficient than this. Visual systems have been developed to form sharp visual images and to collect more light, but it seems that even in fairly rudimentary eyes the ability to respond to a photo-chemical reaction is developed to a point not much above the physically possible limit.

## SUMMARY

1. It is important that all the information which can be obtained from experiments on visual sensitivity should be made available. Methods of experimentation and calibration are described which can lead to measures of spectral and absolute sensitivity in energy units.

2. Experimental determinations of spectral and absolute sensitivity are discussed for the cases of five species—man, the cat, the long-eared owl *Asio wilsonianus*, the toad *Xenopus laevis*, and the aquatic flatworm *Dendrocoelum lacteum*.

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